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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

Fides enim certa non provenit ex auditu.

Frederick II of Hohenstaufen

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 *Penionzhkevich* (1945) metabolic differences exist between eggs developing under either natural or artificial incubation conditions.

Experimentation by man with artificial incubation was far antedated 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*, 1930 a and b; *Barrett and Crandall*, 1931; *Groebbels*, 1937; *Frith*, 1959). Only a brief survey of the pertinent facts can be given here.

Eulipoa wallacei, 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 hoeskeri* 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 *Melipoo* 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 maleo* and of *Megapodius hueskeri*. But much more complex incubating arrangements are made by the other two *Megapodius* 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 lathamii*, 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 lathamii*, *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 (Groebhels 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; *Gowe*, 1950; *Krizenecky, Sajner, Orel 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 Maoling 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 *Martin de Herrada* who, accompanied by *Geronimo Marin* 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

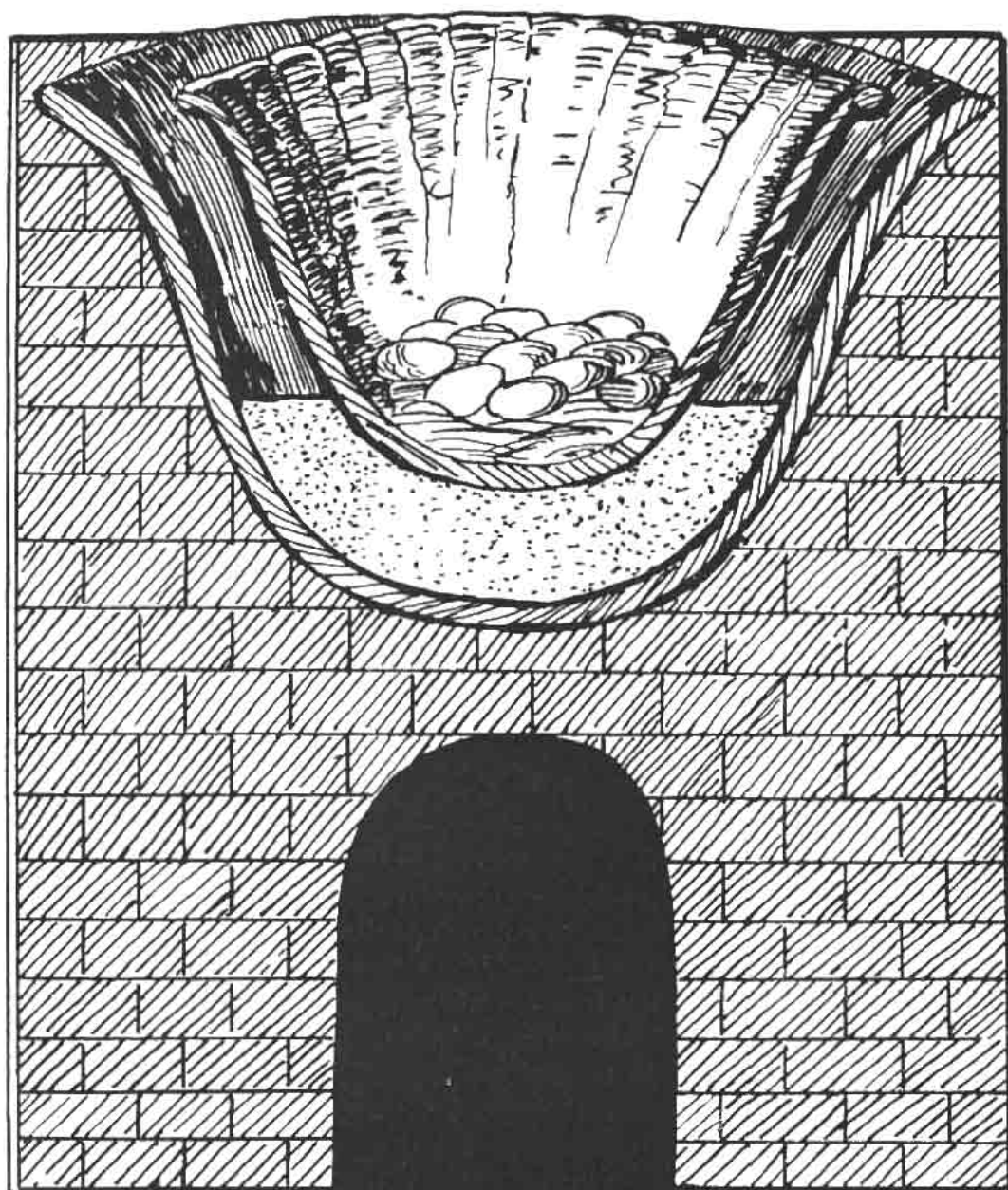


Figure 1

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 seeke new inuentions to get their liuing, to relieue and supply their necessities. So that many of this kingdome, seeing the whole countrie so thoroughly 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 aforesaide), where they have their whole families vnder borde to defende them from the sunne

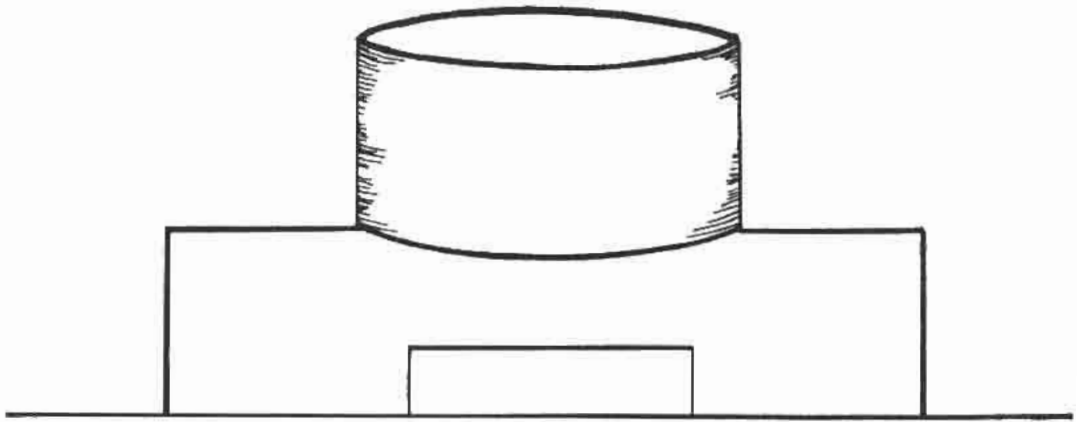


Figure 2

Vertical section of a Chinese incubator similar to that shown in Fig. 1.
Removable top cover not shown (*From R. Saint-Loup, 1895*).

and rayne, and inclinations of the heauens. There they do vse 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 barkes so great quantitie of duckes, that they sustaine a great part of the countrey therewith; and the vse thereof is as followeth."

"They haue cages made of canes so bigge as the vpper most holde of the barke, in the which may be foure thousand duckes at once. They haue in certaine places of these cages made nestes, where these duckes do almost euery 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 duckes, which is verie warme, where they leaue them so many dayes as experience hath taught them that they will come foorth. Then they doo take them out of the doong, and do breake them one by one, and take a little ducklin, the which they do with so great cunning that almost none of them doth perish, which is y^t 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 vse an artificall helpe: to giue a little warmenes vnto the doong for the bringing forth of their egges, they do vse then an other inuention as ingenious as the first, and that is this: they take a great number of canes tied one by another, whereon they do laye the doong, then vppon that they doo lay their egges, and do couer 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 readie 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 liuing is greatly vsed in all that countrie, and verie profitable, for that it is a victuall most vsed 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 hatching 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 (*Fronza*, 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 (*Fronza*, 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 trundle 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 *Fronza*. 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. *Bruyerin* (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 Camels 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 foure hundred living Chickens, and where defection is, every sharer beareth a part of the losse, for the Hatcher or Curator, is onely Recom-pensed 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. *Bruyerin* (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 Syracuse, 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 nourses, 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 eggs 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 eggs must be turned with a man or womans 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 entitled: *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 respondeat ignis calorem nihil posse generare, ut in prioribus libris demonstratum est: respondere posset, in Aegypto ova excludi ignis calore, quod ab omnibus affirmatur: ita dicet, ex imperfecto metallo, vi ignis, perfectum, ut ex ovo 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. 3). 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), *Bock* (1577), *Kirchherr von Suchen* (1584), *Benedictus Pererius* (1595), *Leo Africanus* (1600), *Gesner* (1604), *Radziwill* (1614), *Fürer* (1621), *Ulyssis Aldrovandi* (1645), *la Boullaye* (1657), *Vesling* (1664), *Monconys* (1665), *della Valle* (1672), *Thévenot* (1674), *Graves* (1675), *Melton* (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 *Robynson* (1556): "They brynge up a greate multitude of pulleyne, and that by a meruaylouse policy. For the hennes dooe not sytte vpon the egges: but by keepynge theym in a certayne 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 steade 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), *Le Bruyn* (1725), *Chomel* (1725), *Sicard* (1729), *Myller* (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), *Iane* (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 Pouge-Réal, the pleasure home of *Alphonse II*, King of Naples:

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

Aussi a ung four à oeufs couvrir,
Dont l'on pourroit, sans geline, eslever
Mille pousins, qui en auroit affaire,
Voir dix mille qui en voudroit 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."

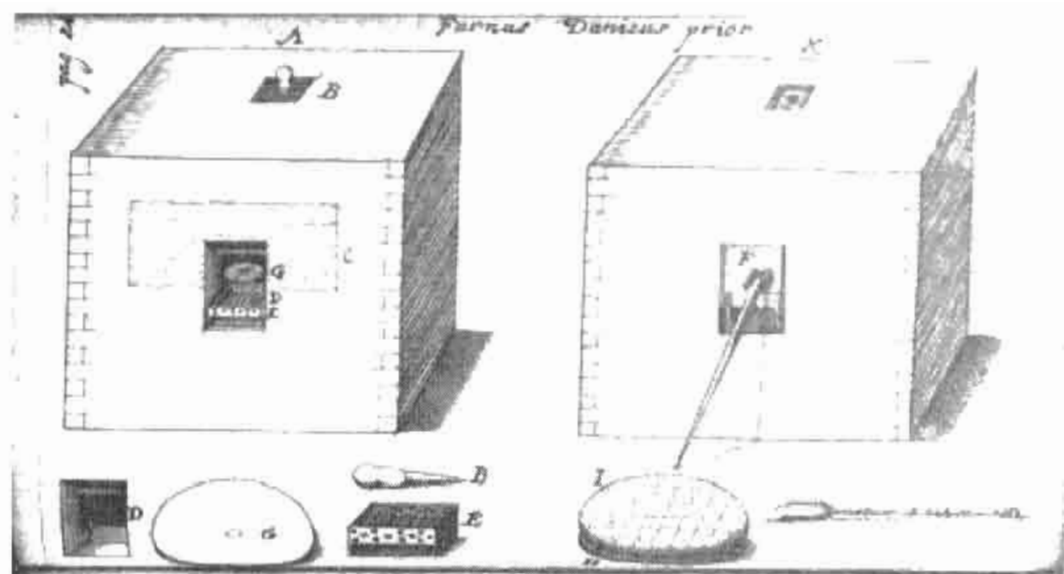


Figure 4

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 "Gallinoculture 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 gurgeons 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 advise 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 Hogshhead, 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 lye 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 hatcht 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 weiks, 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 hatchd, 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 adde 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 parment, 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*



Figure 5

Portrait of Cornelis Drebbel (From *Tierie*, 1932).

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 Minories by Dr. Keffler's brother (actually Kuffler'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 Alckmaar, *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).

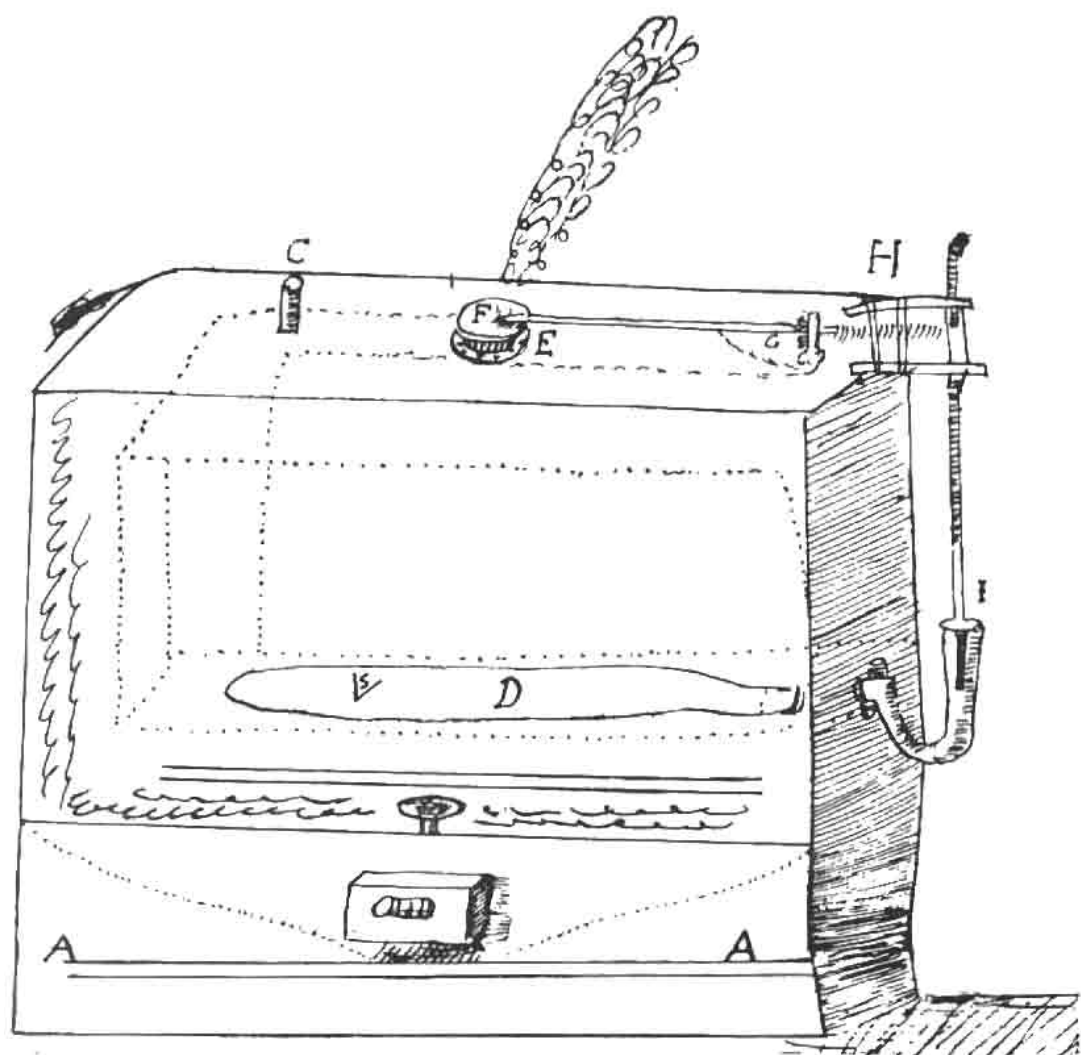


Figure 6

Drebbel's incubator with mercury-alcohol thermostat (From manuscript 2206, Ll. V 8, Part II, I 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 *Drebbel'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 & difficultie. this Furnace must Bee without A grate having 2 or 3 holes. running from the Place where the Δ is to the Edges which Blow the Δ as A over the Δ 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 Bot-tome & Topp the ∇ is put with which it must Bee filled thro a small Pipe Comeing out of the Topp of the Furnace as C & still as the ∇ water wasts (wastes), itt must Bee filled Againe thro the same in the Bottome of the water Box. Between the Double of itt Lay the glass D: which is filled with \S to the Neck & in the Necke ϕ . to fill this Retorte you must first Put the ϕ in, then the \S , then Turne itt upside downe, holding to the Mouth & the ϕ will come into the neck. Let the Δ 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 playying upon A Crosse Pinn att G & at H. It hath A Screw By which meanes 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 re-torte as at I: See that when the Δ groweth hotter the (read "than") ordinary the \S expands itt selfe pressing upon the ϕ & the ϕ the Pinn I & So closeth the hole E & dampe the Δ till It comes to A just ("proper") heate."¹

Drebbel'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:

Δ fire, ∇ water, \S alcohol, ϕ 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 balneum 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 falso", *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 superficies 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 superficies of the Oyl, shall not be deserted by the said Superficies till the whole quantity be consumed."

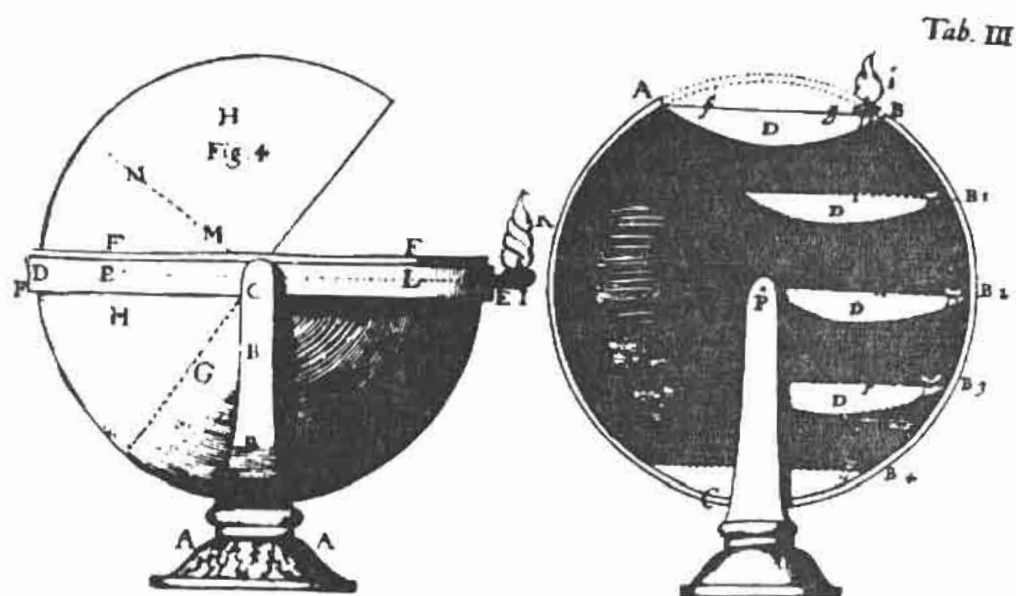
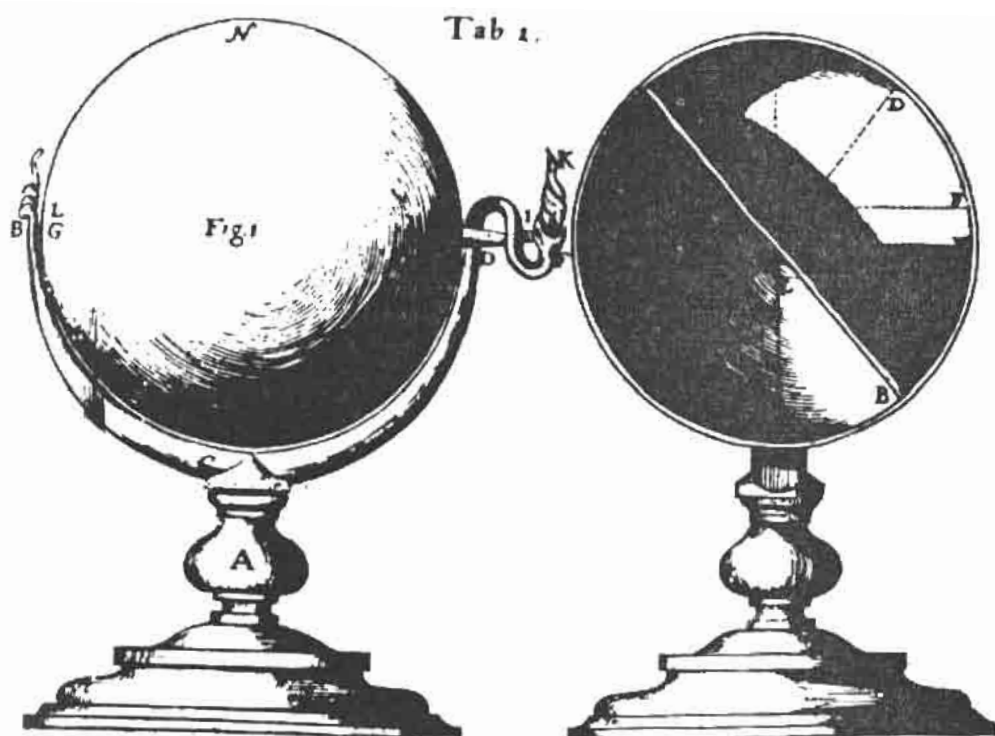


Figure 7

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).

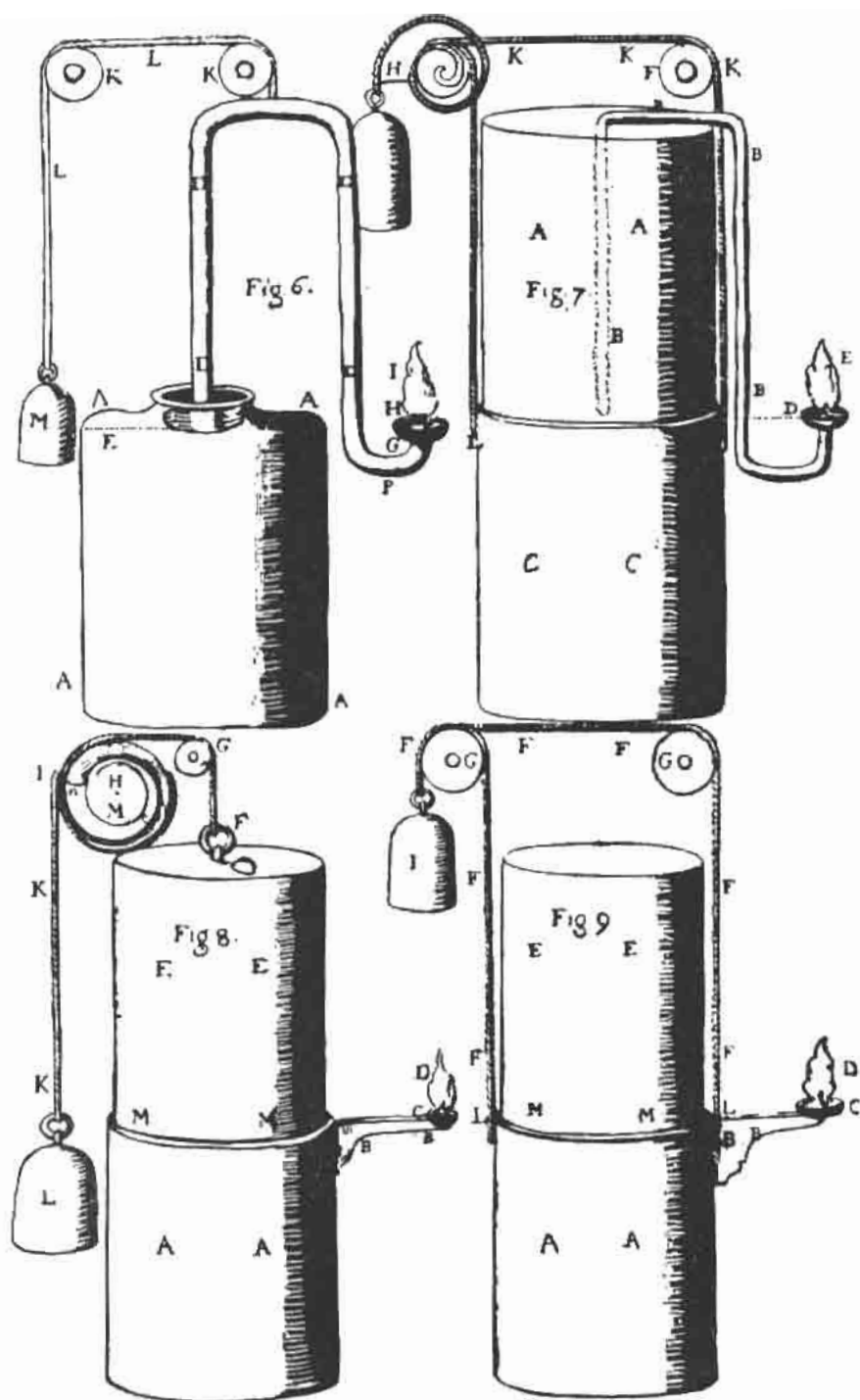


Figure 8

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*).

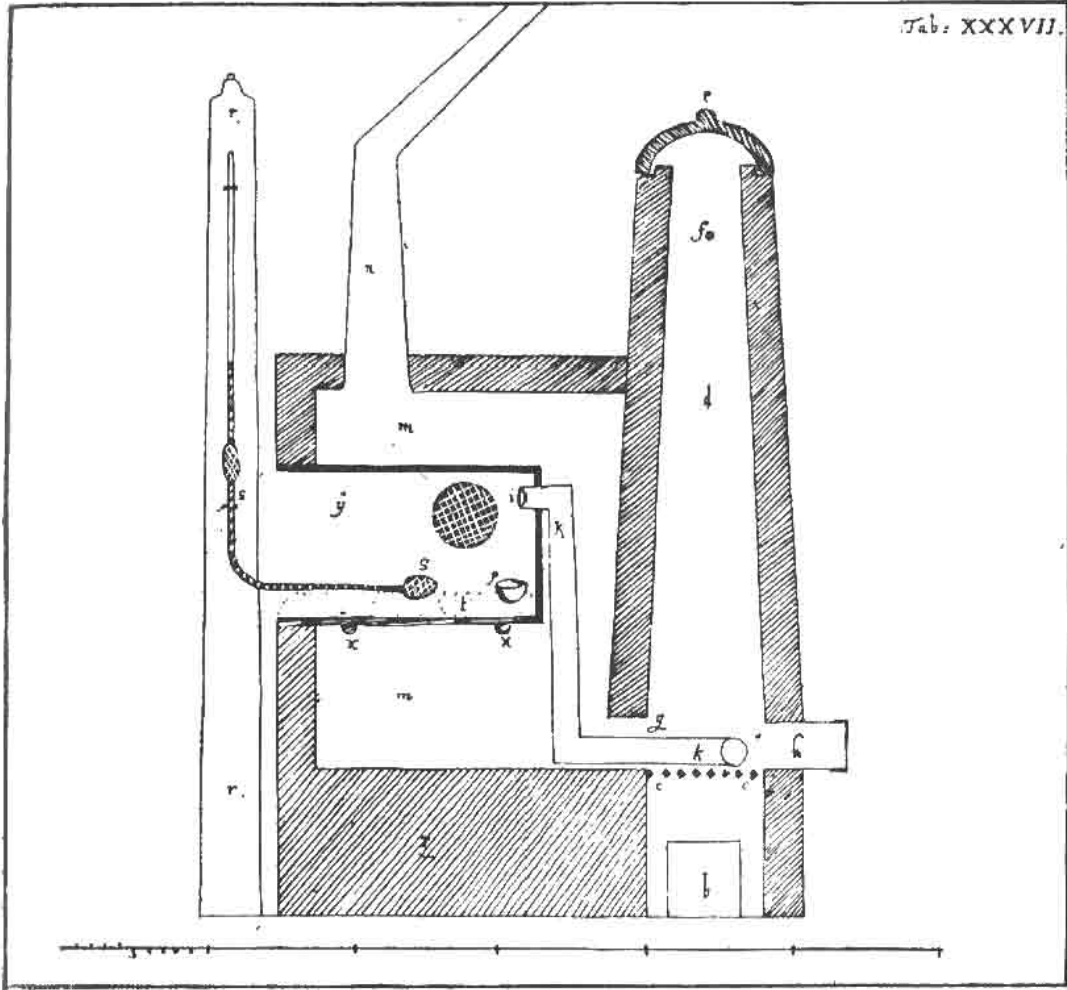


Figure 9

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 satisfie our selves herein, it were well we made our remarcks 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 severall 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 Buono* 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 sheetiron 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.

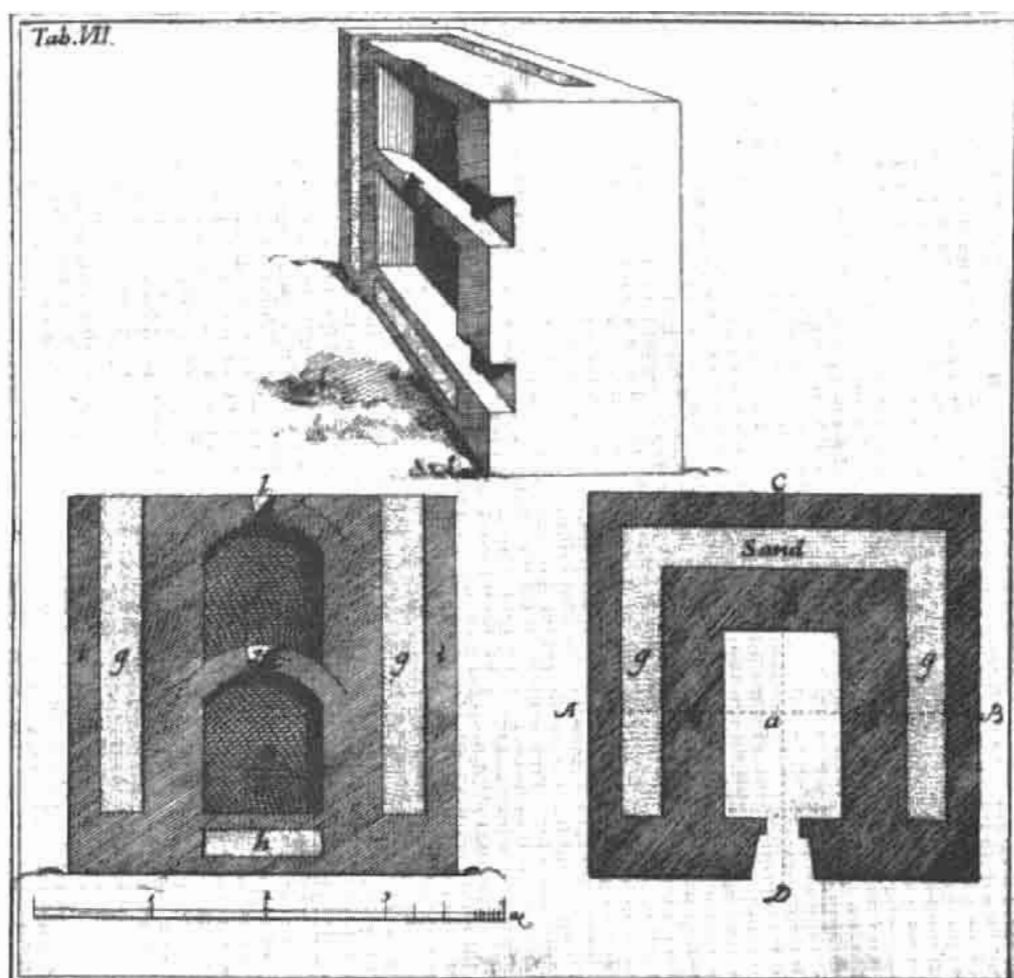


Figure 10

Hatching ovens as illustrated by *Cederhielm*. a, lower oven width 1 yard, depth $6\frac{1}{2}$ feet, height 1 yard 7 inches; b and c, inner and rear wall, each $\frac{1}{2}$ yard thick; d, door of lower oven 8 inches wide, 9 inches high; e, door of upper oven somewhat smaller than that of lower; f, upper oven with same width and depth as lower, but only 1 yard high; g, sand fill, 9 inches deep; h, underneath hatching area dry and solid supports $\frac{1}{2}$ foot in diameter; i, side walls $\frac{1}{2}$ foot thick; k and l, dampers of lower and upper oven. (From *Cederhielm*, 1748.)

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 Péatieux* (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 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). *Féry-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 *Foucault* 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 hothouses — 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; *Chevallier*, 1831), and it became well established in the community of Chaudes-Aigues (Departement 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 (Departement 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-*

main. *Bonnes'* 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.

Delpsch 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),

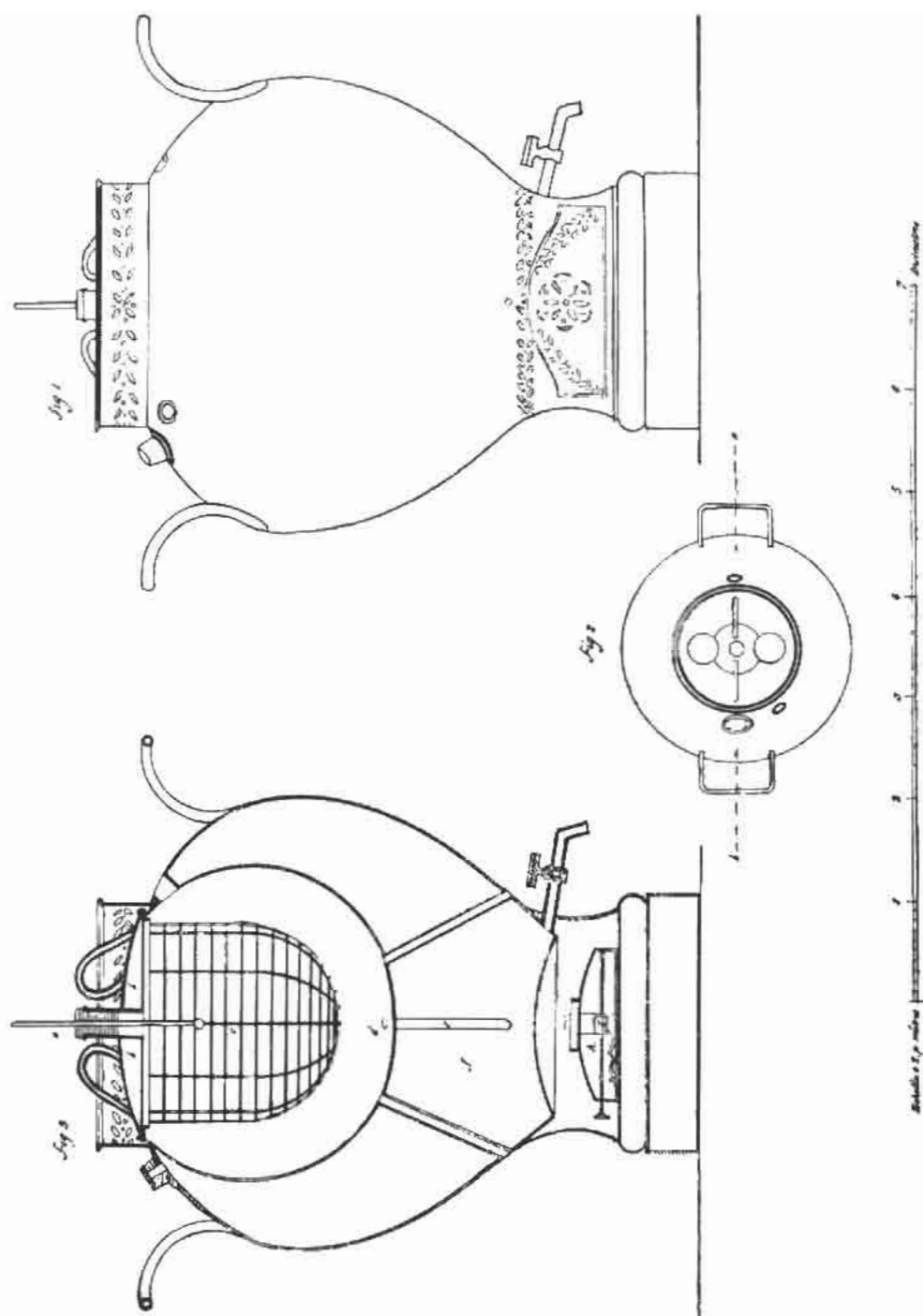


Figure 11

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).

Gobin (1882), *Halsted* (1883), *Stoddard* (1886), *Roullier-Arnoult* (1889), *Wright* (1890), *Lewer* (1911) and *Banner* (1916).

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 resolve 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 Lavisson*, 1862; *Dareste*, 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° 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 I. 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

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 heran und durchzieht, welches den Fortschritt hindert, sogar öfters lähmt. - - - 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."

Table 1

Age of eggs when set Days	Number of eggs	Percentage of fertile eggs hatched
1-7	3253	76.2
8-14	930	74.0
15-21	109	64.6
22-28	61	32.0
29-31	19	0

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 63.5 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

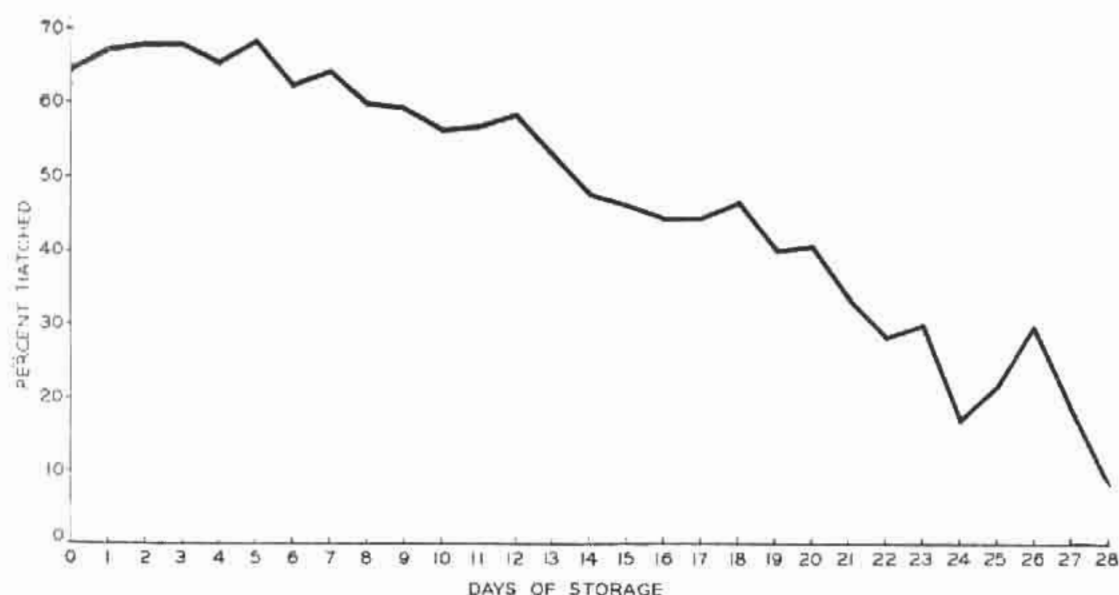


Figure 12

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 Bearnse* (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 Bearnse* 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 99¾° 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 1735 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 c) 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 (*Colasanti*, 1874-1875; *Pictet*, 1893; *Rabaud*, 1899; *Mancini*, 1908; *Mauro*, 1922; *Dougherty*, 1926-1927; *Jull, McCartney, and El-Ibiary*, 1948). 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 (*Mussehl 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*, 1948). 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* (1943), *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.

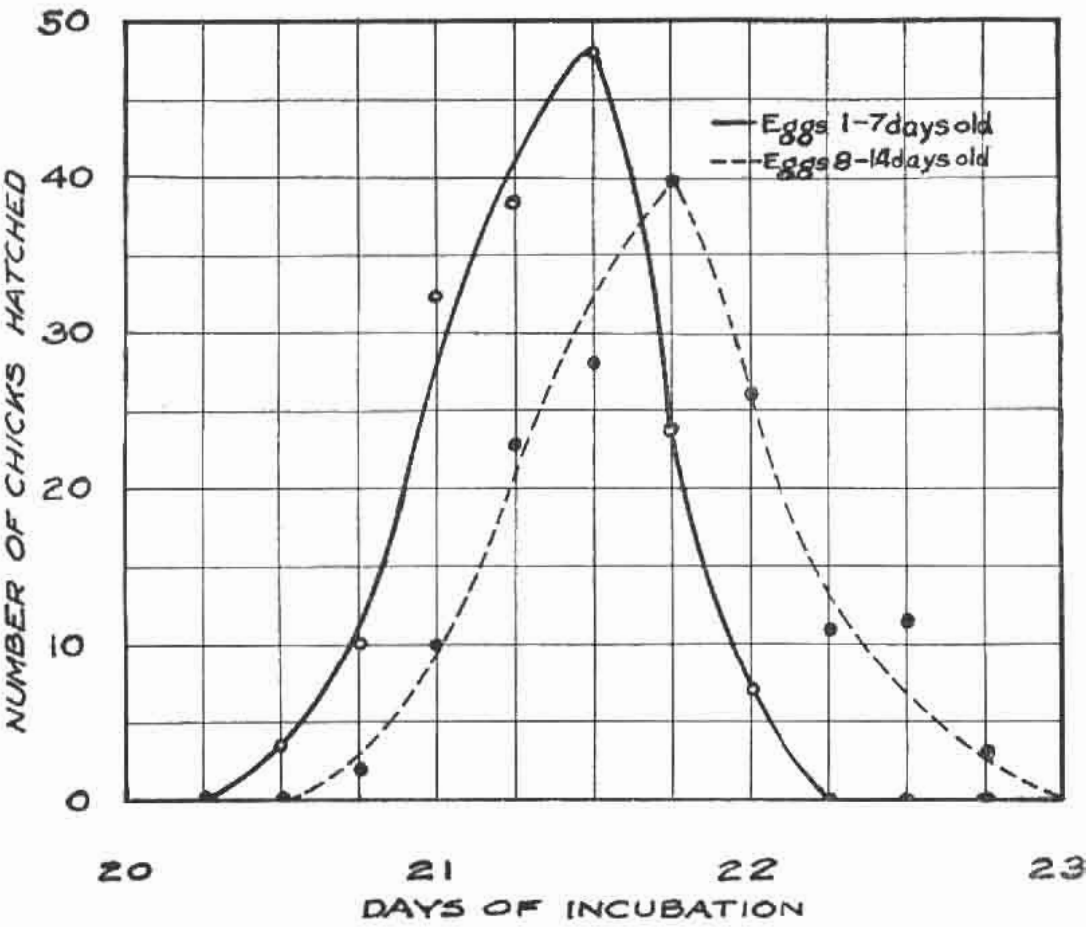


Figure 13
The effect of age (time of storage) of eggs on length of the incubation period (From *Funk*, 1934 a).

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 2

Test	Age of eggs Days	Time required for incubation in hours	
		Range	Mean
I	1-7	492-528	512
	8-14	498-546	522
	15-17	516-546	530
II	1-7	498-540	513
	8-14	504-540	518
	15-21	510-540	527

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 *Ogorodniy*, 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 poultrymen 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 rumplessness, 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 rumplessness, 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 rumplessness 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 rumplessness occurred either sporadically or after shaking. Since rumplessness (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; *Féré*, 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* (1936 a), can be lowered by as much as 5° F. (3° C.) without ill effects. According to *Kotliarov* (1936 a) 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, Gunns and Moses* (1933) cooling for 12 hours to about 70° F. (21° C.) reduced the hatch by only 3.4 per cent. *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 *Prützker* (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* (1948 b) it may lead to disharmonious growth of various organs, ending in death of the embryos.

Taylor, Gunns 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

-3°C . (26.6°F .). 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°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°F . (-23°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°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-Ange*, 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

Relative humidity %	Loss of weight of eggs %	Fertile eggs hatched %
70-80	5.3	45.5
60-70	8.7	62.1
50-60	9.8	69.3
40-50	10.2	68.6
30-40	11.5	68.6
20-30	14.5	60.6
15-20	17.4	48.0

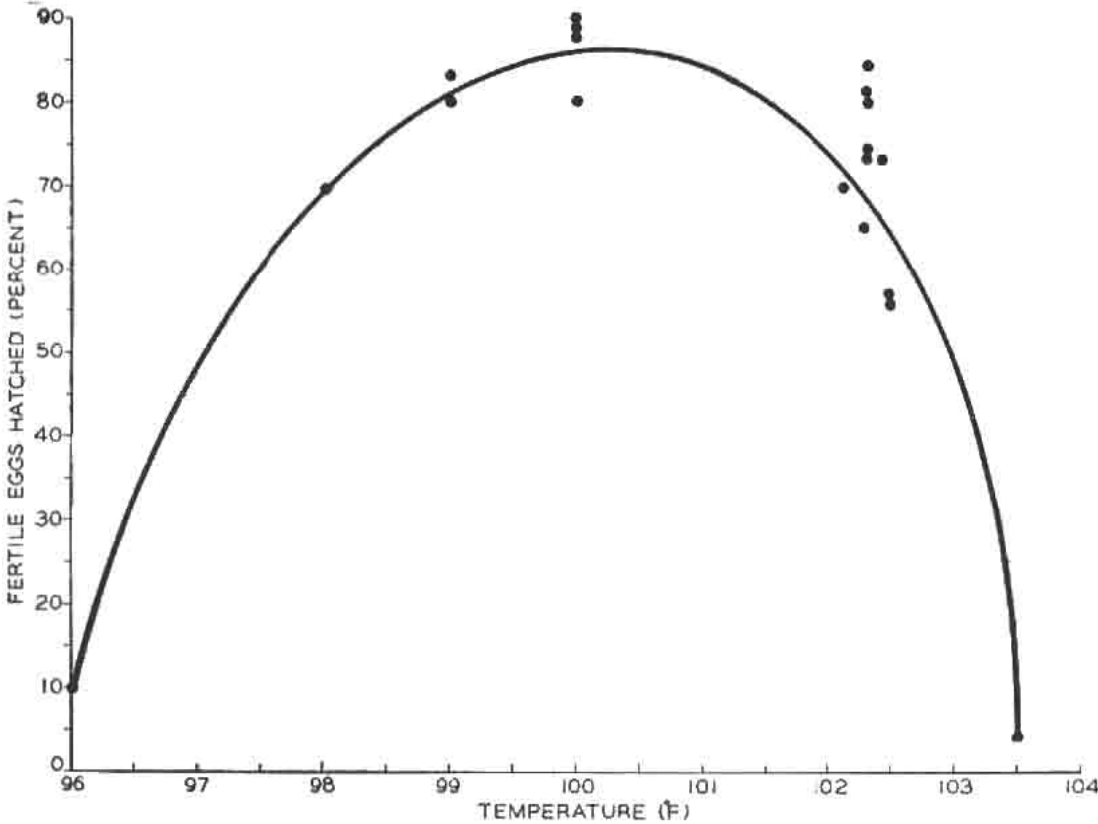


Figure 14

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.

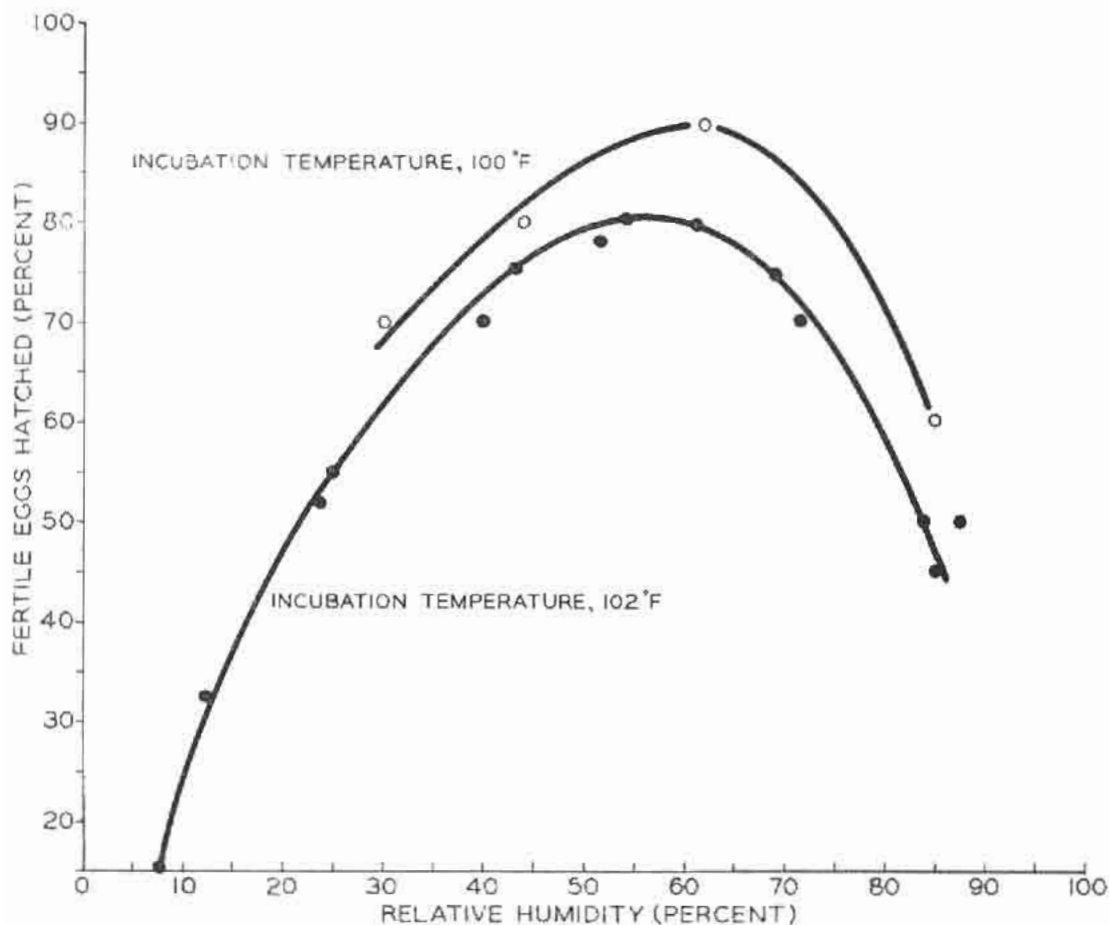


Figure 15

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

Coefficients of correlation between hatchability of eggs and the relative humidity of the incubator room during various periods of incubation.

	<i>Day of hatching</i>	<i>Humidity during stated periods</i>		
		<i>7 days prior to hatching</i>	<i>14 days prior to hatching</i>	<i>21 days of incubation</i>
Correlation coefficient	.31	.55	.69	.68
Standard error	.18	.14	.10	.11

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, *Aggazzotti*, 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. *Townsend* (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 *Otrygan'ev and Kuchkovskaia* (1941) and *Otrygan'ev* (1941a) 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'iakova (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 (*Liharzik*, 1858). *Byerly 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. *Chattock* (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 (465 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 Watterson* (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.

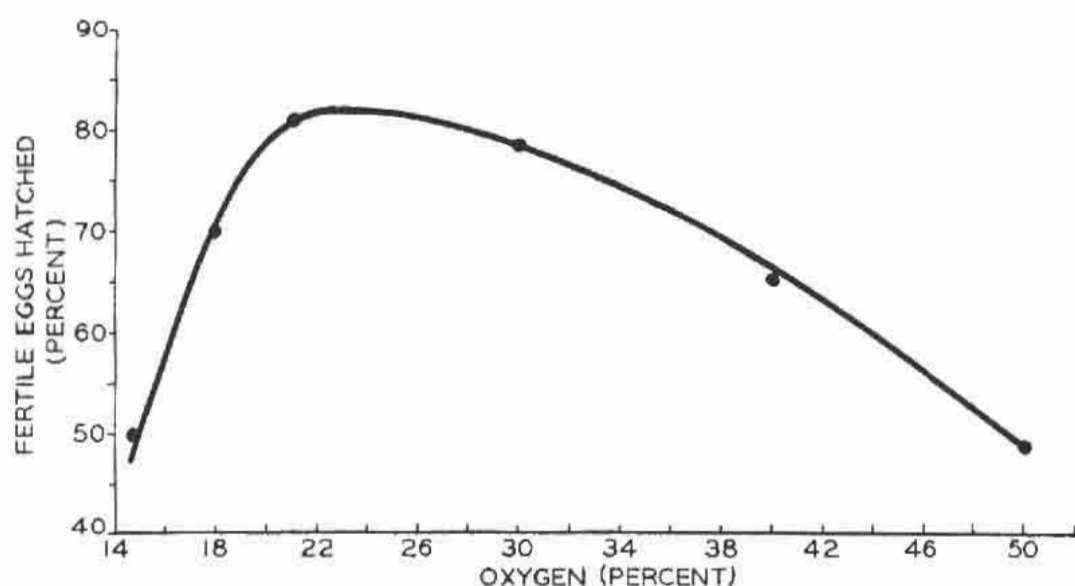


Figure 16

The effect of oxygen during incubation on percentage of fertile eggs hatched. Temperature 99°F., relative humidity 70 percent, carbon dioxide below 0.5 percent. (From *Barott*, 1937).

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 Gunns* (1956). Their principal results, in their own words, were as follows: "Normal hatchability resulted from CO_2 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 CO_2 levels. No level of CO_2 consistently produced significantly better hatchability than the control incubators operating at 0.05 to 0.12 percent CO_2 . Reduction of the period of exposure to the first 24 or 48 hours of incubation reduced the relative decrease in hatchability associated with high CO_2 levels, but failed to produce any improvement in hatchability over control conditions. O_2 levels below 18 percent tended to reduce hatchability proportionately to the decrease in O_2 concentration. Levels of 18 to 50 percent O_2 produced normal hatchability. Increasing O_2 concentration to 75 percent or higher reduced hatchability significantly. The early chick embryo is very susceptible to conditions of reduced O_2 supply or high concentrations of carbon dioxide; it is very resistant to extremely high concentrations of oxygen. —Commercial incubators tested had O_2 and CO_2 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*,

1933; Sadler, Wilgus and Buss, 1954), that chicken embryos need little, if any, oxygen from outside the eggs during the first two days of incubation (Portmann and Jecklin, 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 5

Egg weight g.	Number of fertile eggs	Fertile eggs hatched %
52-59.9	290	62.06 ± 2.85
60-73.9	93	44.09 ± 5.14

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. *Czarnecka* (1954), *Axelsson* (1954) and *Goles* (1956 b) 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. *Jull 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

Egg weight g.	Number of fertile eggs	Fertile eggs hatched %
40.00-52.99	123	67.48 \pm 3.02
53.00-59.99	992	65.32 \pm 2.00
60.00-66.99	23	52.17 \pm 14.03

The differences in the material analyzed by *Dunn* and by *Jull 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 *Jull 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 F_1 and F_2 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 ± 0.079 g. 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 hatching 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 7

Egg Weight 51-60 g.		Egg weight less than 50 g. or more than 60 g.		Difference
N	Hatch %	N	Hatch %	
3193	66.6 \pm 0.82	1314	58.6 \pm 1.36	8.0 \pm 1.59

egg weight. The percentage hatch for all eggs amounted to 64.3 percent. Deviations from optimum weight were, therefore, responsible for a loss of 1.95 percent of hatchability (65.6 being taken as 100). While deviations from optimal egg weight unquestionably influence hatching adversely, it is also evident that we are dealing with a minor factor in hatchability.

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

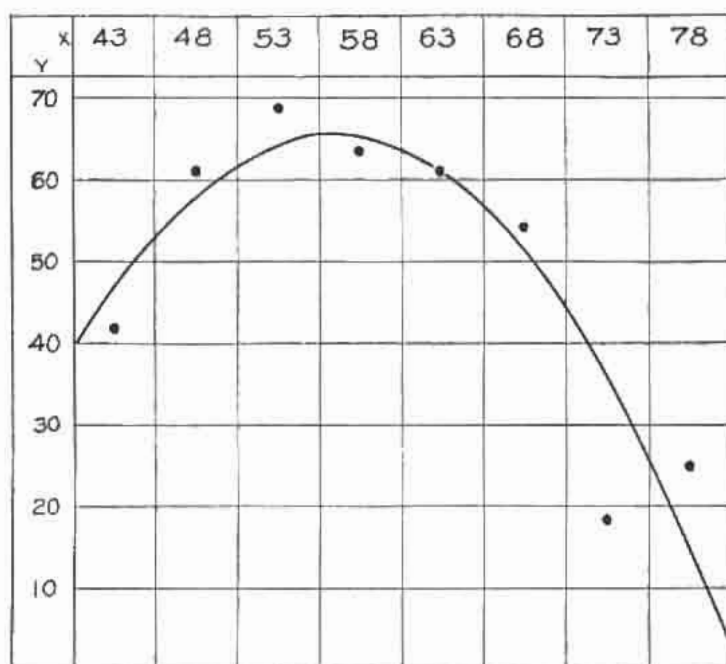


Figure 17

The regression of hatching percentage on weight of eggs. X: egg weight, Y: hatching percentage (From Axelsson, 1932 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

Breed	Number of birds	Egg size		Hatchability of fertile eggs %		Coefficient of correlation
		Mean g.	σ g.	Mean	σ	
White Leghorn	222	53.7	3.7	71.5	17.2	-0.171 ± 0.065
Rhode Island Red	161	56.5	4.6	58.0	19.4	-0.264 ± 0.074

Table 9

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

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 ± 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

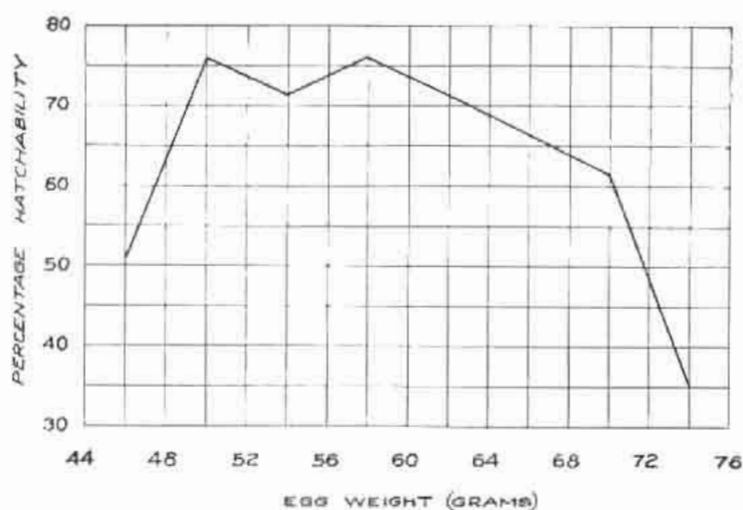


Figure 18

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 *Penionzhkevich* (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 *Penjonschkewitsch*, 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

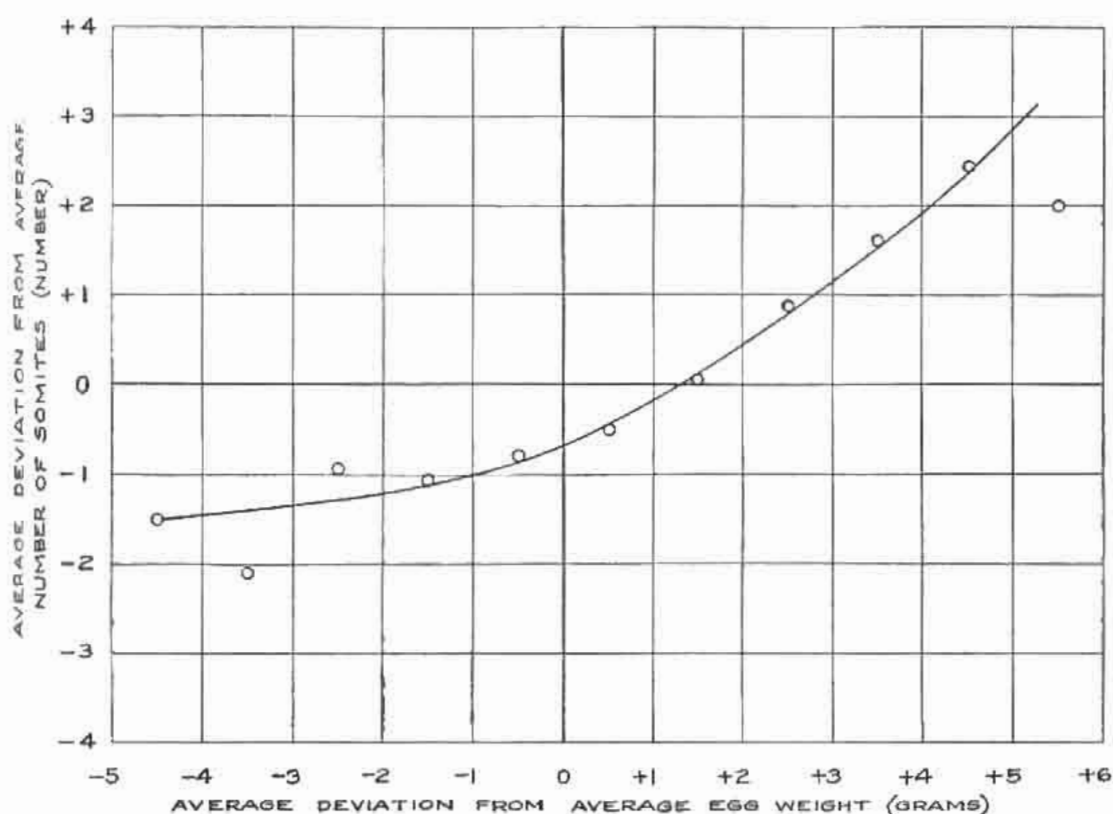


Figure 19

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 10

	Egg length <i>v</i>	Egg breadth <i>v</i>
Average for 12 wild species (unweighted mean)	4.48	2.98
Domestic fowl	4.29	3.79

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 ± 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 *Znojilová, Zoufalý and Pátková* (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 11

Shell thickness in mm	0.18-0.22	0.22-0.26	0.26-0.30	0.30-0.34	0.34-0.38	0.38-0.42
Number of eggs	18	168	668	492	76	12
Percent hatch	61	79	88	80	58	50

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

Table 12

<i>Hen number</i>	<i>Weight lost during 20 days storage %</i>	<i>Weight lost per sq. cm. of surface g.</i>	<i>Number of eggs incubated</i>	<i>Fertile eggs hatched %</i>
146	3.99	0.0368	29	22.0
149	3.60	0.0323	18	47.0
287	4.28	0.0375	13	0.0
342	2.67	0.0214	25	32.0
Mean of normal eggs	1.96	0.0170	250	59.8
Range of normal eggs	1.30-2.79	0.0113-0.0229		

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

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

Table 13

<i>Weight loss %</i>	<i>Number of eggs with living embryos on 14th day</i>	<i>Number of chicks hatched</i>	<i>Hatch from eggs which had living embryos on 14th day %</i>
6.00-8.50	19	13	68.42 ± 10.66
9.00-11.50	55	39	70.91 ± 6.12
12.00-16.50	18	9	50.00 ± 11.79
Total	92	61	66.30

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

that the coefficient of correlation between the percentage of hatch and the average loss of weight amounted to -0.734 ± 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.

Table 14

Number of hatch	Date of setting eggs	Number of fertile eggs set	Hatch %	Loss of weight in g.	
				M	σ
I	Jan. 29	380	76.1	0.131	0.0151
II	Feb. 9	459	74.9	0.133	0.0295
III	Feb. 19	404	75.0	0.136	0.0280
IV	March 3	478	63.6	0.140	0.0370
V	March 13	366	60.1	0.161	0.0543
VI	March 29	176	48.3	0.172	0.0527
VII	April 9	201	44.8	0.159	0.0465
VIII	April 20	302	65.6	0.135	0.0305
X	May 11	348	58.3	0.142	0.0285
M			63.0 ± 3.80	0.145 ± 0.0051	0.0358 ± 0.0043
σ			11.4 ± 2.69	0.0152 ± 0.0036	0.0130 ± 0.0031

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

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

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

Pore width in μ	0-6	6-12	12-18	18-24	24-30	30-36	36-42
Number of eggs	0	48	168	411	315	93	42
Percent hatch	—	38	66	82	90	81	64

Table 17

Pore width in μ	0-5	5-10	10-15	15-20	20-25	25-30
Number of eggs	15	48	399	264	66	21
Percent hatch	40	75	78	51	55	29

Table 18

Weight loss %	0.05-0.10	0.10-0.15	0.15-0.20	0.20-0.25	0.25-0.30	0.30-0.35
Number of eggs	6	312	804	372	54	12
Percent hatch	50	75	77	72	56	25

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 dif-

Table 19

Breed or cross	1930		1931	
	N	Average actual loss of weight per egg, g.	N	Average actual loss of weight per egg, g.
White Leghorn	314	0.127	395	0.134
Rhode Island Red	336	0.137	288	0.146
Barnevelder	223	0.143	488	0.160
(Wh. Leghn. ♀ x R.I.R. ♂) F ₁	383	0.124	88	0.134
(R.I.R. ♀ x Wh. Leghn. ♂) F ₁	105	0.116	137	0.125
(Wh. Leghn. ♀ x Barnev. ♂) F ₁	119	0.134	93	0.156
(Barnev. ♀ x Wh. Leghn. ♂) F ₁	66	0.131	281	0.131
(R.I.R. ♀ x Barnev. ♂) F ₁	113	0.136	27	0.161
(Barnev. ♀ x R.I.R. ♂) F ₁	136	0.130	95	0.145

ference 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, proffered 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 Cruickshank* (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

Table 20

Cross	Weight loss of eggs g.	
(Wh. Leghn. ♀ x R.I.R. ♂) F ₁	0.137 ± 0.0013	
(R.I.R. ♀ x Wh. Leghn. ♂) F ₁	0.123 ± 0.0012	
Difference	0.014 ± 0.0018;	$\frac{D}{e(D)} = 7.78$
(Wh. Leghn. ♀ x Barnev. ♂) F ₁	0.143 ± 0.0029	
(Barnev. ♀ x Wh. Leghn. ♂) F ₁	0.131 ± 0.0012	
Difference	0.012 ± 0.0033;	$\frac{D}{e(D)} = 3.64$
(R.I.R. ♀ x Barnev. ♂) F ₁	0.157 ± 0.0032	
(Barnev. ♀ x R.I.R. ♂) F ₁	0.139 ± 0.0024	
Difference	0.018 ± 0.0040;	$\frac{D}{e(D)} = 4.50$

the eggs laid by F₁ hens. The difference between the F₂ groups amounts to 3.66 times the error.

Axelsson 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. *Axelsson*, therefore, assumes that both sex-linked and auto-

Table 21

	Number of eggs	F_2 Hatchability %
F ₁ hens from matings in which the breed with lowest weight loss and highest hatching percentage was maternal (Wh. Leghn. x R.I.R.; Wh. Leghn. x Barnev.; R.I.R. x Barnev.)	823	57.8 ± 1.72
F ₁ hens from matings in which the breed with lowest weight loss and highest hatching percentage was paternal (R.I.R. x Wh. Leghn.; Barnev. x Wh. Leghn.; Barnev. x R.I.R.)	820	66.5 ± 1.65
Difference		8.7 ± 2.38

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 (+.363) 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

Cross		Weight loss of eggs g.	
Rhode Island Red (Wh. Leghn. ♀ x R.I.R. ♂) F ₁		0.144 ± 0.0022	
		0.137 ± 0.0013	
	Difference	0.007 ± 0.0026;	$\frac{D}{e(D)} = 2.69$
Barnevelder (Wh. Leghn. ♀ x Barnev. ♂) F ₁		0.160 ± 0.0018	
		0.143 ± 0.0029	
	Difference	0.017 ± 0.0031;	$\frac{D}{e(D)} = 5.00$
Barnevelder (R.I.R. ♀ x Barnev. ♂) F ₁		0.160 ± 0.0018	
		0.157 ± 0.0032	
	Difference	0.003 ± 0.0037;	$\frac{D}{e(D)} = 0.81$
(Barnev. ♀ x Wh. Leghn. ♂) F ₁		0.131 ± 0.0012	
(R.I.R. ♀ x Wh. Leghn. ♂) F ₁		0.123 ± 0.0012	
	Difference	0.008 ± 0.0017;	$\frac{D}{e(D)} = 4.71$

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* (1942 a) 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; *Bryant 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

Porosity index*			Mean percentage hatchability
Range	Mean	Number of hens	
6.99 and below	6.25	80	70.0
7.00 — 7.99	7.35	64	69.5
8.00 and above	8.89	50	69.6

*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. Serebrowsky* (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 *Mussehl 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,

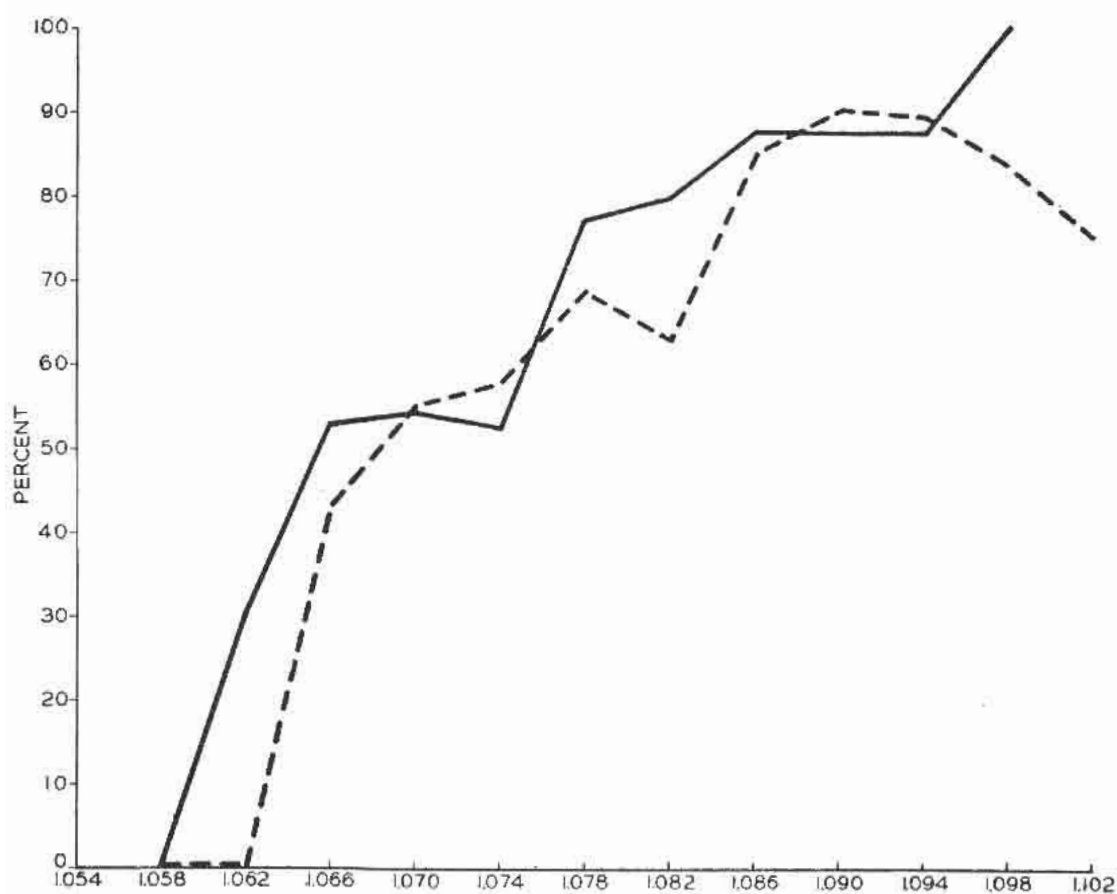


Figure 20

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

<i>Date when eggs set</i>	<i>Group</i>	<i>Number of eggs</i>	<i>Infertile %</i>	<i>Mortality to 18th day %</i>	<i>Mortality after 18th day %</i>	<i>Hatched %</i>
March 14	I	76	10.5	7.9	15.8	65.8
	II	69	16.0	16.0	27.5	40.6
	III	19	5.3	31.6	42.1	21.0
March 28	I	58	12.1	12.1	12.1	63.8
	II	42	7.1	21.4	35.7	35.7
	III	17	11.8	29.4	41.2	17.7
April 11	I	78	14.1	17.9	24.4	43.6
	II	59	0	20.3	22.0	57.6
	III	18	16.7	61.2	22.2	0

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 contradistinction 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

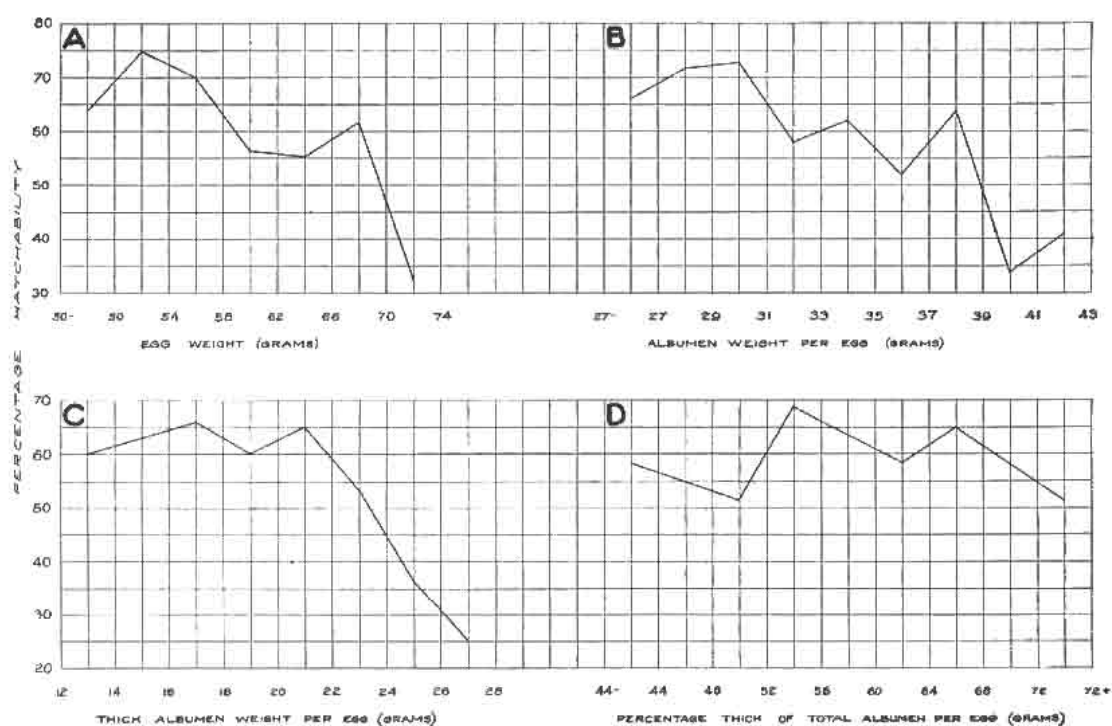


Figure 21

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 Wagenen* (1935), *van Wagenen and Hall* (1936) and *Hall and van Wagenen* (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 Wagenen*, 1936; *Brockhuizen, 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 Wagenen*, 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 Wagenen*, 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 *Bisbey, 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 Mecchi* (1939), *Polk and Sipe* (1940), *Hart and Stuart* (1944), *Temperton and Dudley* (1946-1948), *McClymont and Hart* (1948), *Kolqataj* (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 units¹ 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 25

Date of hatch	No-alfalfa group: 224 units vita- min A fed per day Hatch %	4%-alfalfa group: 336 units vita- min A fed per day Hatch %	8%-alfalfa group: 444 units vita- min A fed per day Hatch %	Estimated units of vitamin A per gram of egg yolk		
				No-alfalfa group	4%-alfalfa group	8%-alfalfa group
May 1, 1933	13.8	31.3	33.3	11	13	14
June 9, 1933	47.0	50.2	60.2	8	15	14
Average	38.4	46.0	52.4	9.5	14	14

ciently severe to interfere with health and normal physiological functions of the laying hens. *Rubin and Bird* (1942) similarly stated that more vitamin A is needed for maximum production than for optimal hatchability. According to *Lissot and Caridroit* (1941) the minimum amount of vitamin A in an egg, necessary for hatching, is 350 international units. *Boelum* (1948) estimated that the daily minimum requirement of Brown Leghorn pullets for good hatchability is 400 units of vitamin A, and

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 dwarfing 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 Bauernfeind* (1942) 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 Bauernfeind* (1942) obtained a similar curve of embryonic mortality, but made the important observation that riboflavin depletion occurred

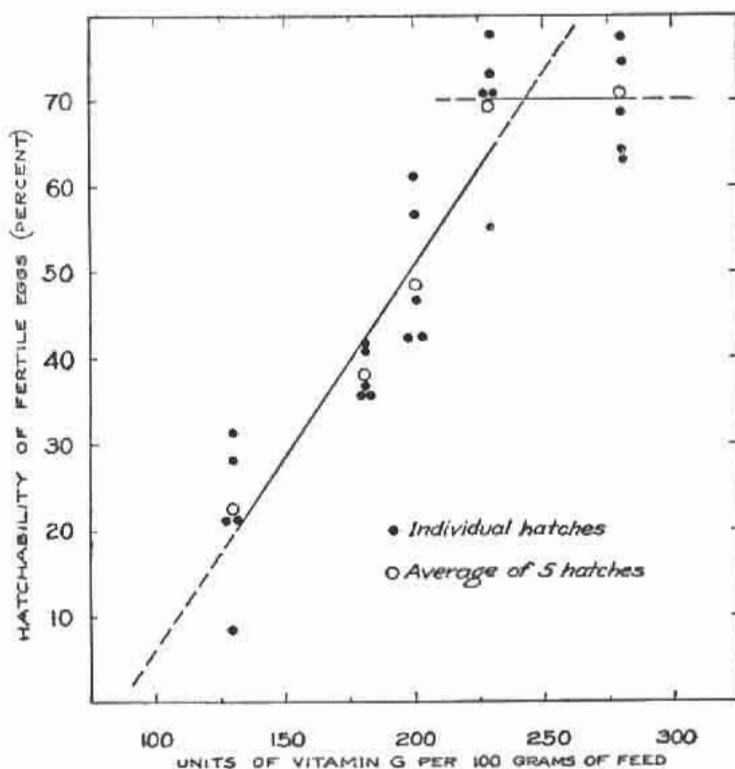


Figure 22

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 inadequate by Petersen, Lampman and Stamberg (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 Ariyoshi (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

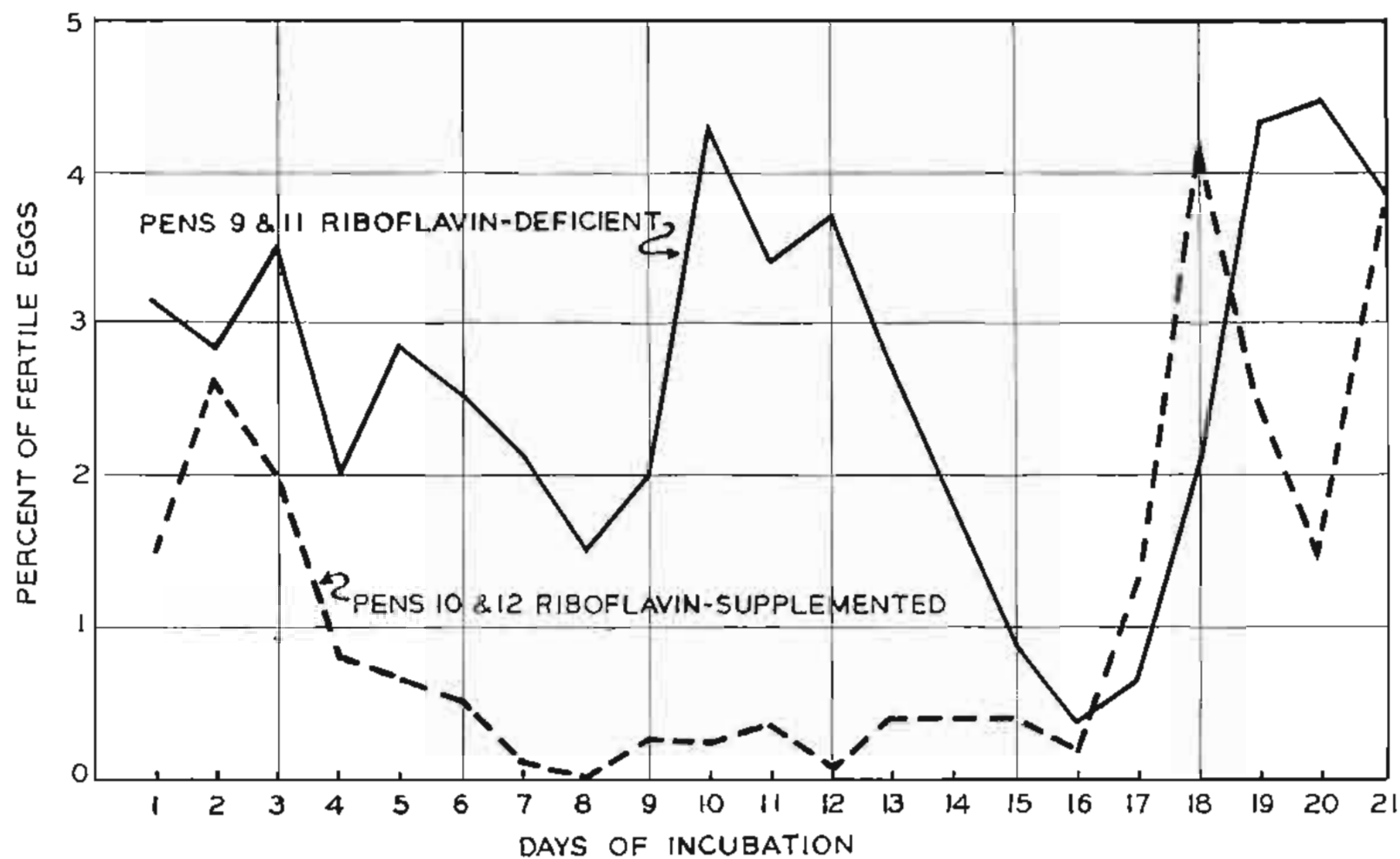


Figure 23
Distribution of embryonic mortality on rations with and without riboflavin.
(From Lepkovsky, Taylor, Jukes and Almquist, 1938).

Cravens, Halpin and McGibbon (1946). 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-aminonicotinamide, 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-aminonicotinamide. Moreover, the effects of both 3-acetylpyridine and 6-aminonicotinamide 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 *Cravens, 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 *Cravens 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 (pteroyl-glutamic 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 un-supplemented diet hatchability dropped to zero by the end of the sixth week, but returned to a normal level when 0.4 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 toward 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 percent 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, Elvehjem and Halpin, 1948 b*).

Vitamin B₁₂ is essential for good hatchability (*Lindstrom, Moore, Petersen and Wiese, 1949; Petersen, Wiese, Lampman and Dahlstrom, 1950; Lillie, Denton, Olsen and Bird, 1950; Olcese, Couch and Lyman, 1949, 1950; Olcese and Couch, 1950; Carver and McGinnis, 1950; Milligan and Combs, 1950; Petersen, Lampman and Wiese, 1950; Couch, Olcese, Sanders and Halick, 1950; Black, Getty, Coates, Harrison and Kon, 1950; Savage, Turner, Kempster and Hogan, 1952; Petersen, Wiese, Dahlstrom and Lampman, 1952; Petersen, Lampman and Wiese, 1952; Sunde, Halpin and Cravens, 1952; Berg, Bearse, McGinnis and McClary, 1952; Mehring, Titus and Waddell, 1954; Arscott, Shorb and Boggs, 1955*).

Vitamin B₁₂ 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 B₁₂, will support very satisfactory hatchability (*Skinner, Quisenberry and Couch, 1951*). *Hill, McConachie, Gartley and Branion (1950)* observed that on a diet deficient in vitamin B₁₂ 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 B₁₂-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 B₁₂-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 B₁₂-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 B₁₂-deficient diets hatchability can be improved by injecting vitamin B₁₂ into the yolk sac; injection into the albumen has no effect (*Kállai, Aros, Biskup and Kralovánszky, 1956*). Analogs of vitamin B₁₂ interfere with normal development (*Coates, Davies and Harrison, 1960*).

Experiments conducted by *Peeler, Miller, Carlson, Norris and Heuser (1951)* demonstrate, however, that after prolonged vitamin B₁₂ deficiency of laying hens, embryo mortality may occur so early as to simulate infertility. Vitamin B₁₂-deficiency is responsible for a marked decrease in

phospholipids, especially cephalin and sphingomyelin, in the embryo (*Yesair, McOsker and Daniel, 1959*), and the level of vitamin B₁₂-intake affects the storage of folic acid in the yolk of eggs (*Welch, Perrett, Clements and Couch, 1954*). On a vitamin B₁₂-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 *Gerriets (1960)* reported similar results after using aureomycin supplements in the vitamin B₁₂-deficient diet of growing chicks and *Mariakulandai, 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 B₁₂-deficient diets are presumably the result of changes in the intestinal flora and a consequent stimulation of vitamin B₁₂-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 B₁₂ requirement for good hatchability is about 0.2 γ per 100 grams of feed, and that the embryos needed approximately 2.5 γ 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 γ /kg. feed, but *Mariakulandai and McGinnis (1953)* estimated the need as not over 1 γ /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 γ /kg. vitamin B₁₂ are required, but that in laying cages or on raised wire floors as much as 3.3 to 4.4 γ /kg. may be needed. On a vegetable diet *Johnson (1954)* found that 1 to 2 γ /kg. added vitamin B₁₂ sufficed. *Chin, Anderson, Miller, Norris and Heuser (1958)* reported for White Leghorn hens that in the presence of adequate amounts of riboflavin the B₁₂ requirement was 0.5 to 1 γ /kg. feed, but as much as 2 to 4 γ /kg. if the available riboflavin was inadequate. There were great (genetic ?) differences between hens in the amounts of vitamin B₁₂ 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

	<i>U.S.P. units of vitamin D fed per 100 g. of feed</i>								
	10	19	39	58	78	116	155	0 (range)	39 (range)
Average weight of eggs in g.									
1932-1933	51.0	50.9	51.7	52.7	52.3	52.7	52.3	53.1	52.9
1934-1935		43.1	46.2	48.4	49.8	50.7	50.5	51.2	51.0
Average blood serum calcium of laying hens.									
Calcium in mg. per 100 cc. blood serum.									
1932-1933	18.7	21.4	24.3	24.7	25.5	26.0	25.2	26.6	25.5
1934-1935		21.2	21.9	23.3	24.5	26.2	25.6	27.3	28.2
Average shell weight in % of total egg weight									
1932-1933	6.7	7.0	8.7	8.9	8.8	9.0	9.2	9.1	9.0
1934-1935		6.1	7.3	8.1	8.5	8.9	8.8	9.1	9.2
Average ash content of egg shell in %									
1932-1933	52.1	52.4	53.0	53.3	53.2	53.2	53.2	53.2	53.1
1934-1935		51.7	52.6	53.0	53.2	53.4	53.5	53.4	53.3
Total number of eggs incubated									
1932-1933	131	284	500	500	500	500	500	500	500
1934-1935		41	111	191	290	247	300	300	300
Average % hatch of fertile eggs									
1932-1933	56.4	44.5	74.6	84.5	84.9	88.1	87.8	91.0	83.3
1934-1935		11.1	37.8	77.4	77.7	79.6	74.2	86.5	77.1

support of the conclusion that vitamin K influences embryo survival and hatching.

The presence of vitamin D in eggs is necessary for normal hatchability, 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, Kletzien, 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 Knandel* (1934), *Carver, Robertson, Brazie, 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 Knandel* (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).

Table 27

Day of incubation	Calcium %		Phosphorus %	
	No cod liver oil	2% cod liver oil	No cod liver oil	2% cod liver oil
15	0.79	0.94	1.31	1.54
16	0.82	0.97	1.14	1.20
17	0.93	1.20	1.13	1.25
18	1.11	1.41	1.11	1.29
19	1.18	1.44	1.16	1.31
20	1.37	1.55	1.28	1.38
21	1.07	1.34	0.96	1.01

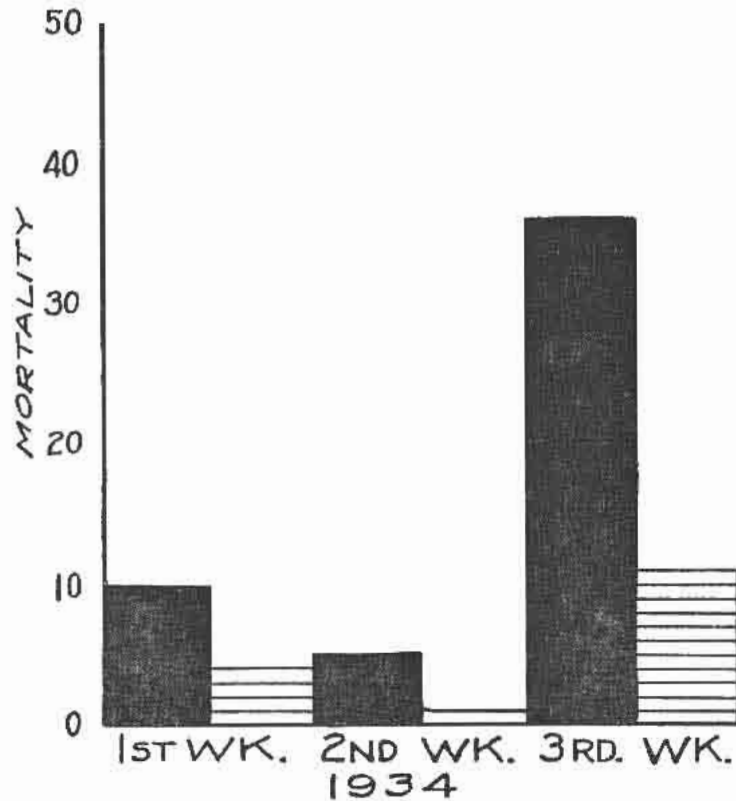


Figure 24

The distribution of embryo mortality in two groups of pen-confined White Leghorns. Shaded: 2 percent cod liver oil; black: no cod liver oil (From *Insko and Lyons, 1936*).

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 (*Branion 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. *Fronza 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, Steenbock, Lepkovsky, Kletzien, Halpin and Johnson* (1925), *Boyd* (1928), and *Kučera* (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 ± 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 ± 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

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

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, Nurnsidze 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;

Barnum, 1935; Ender, 1935; Barbas, 1936). 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* (1941). 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, Cravens, Elvehjem and Halpin* (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, Richey 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 ($3\frac{3}{4}$ 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 Fevold, 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; Pensack, 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 B₁₂ 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, Svacha, 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 $\text{Ca HPO}_4 \cdot 2\text{H}_2\text{O}$ 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 (Blamberg, 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 *Pfaundler (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, Poley 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 $2\frac{1}{2}$ 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. *Gruenwald* (1958) made a histological study of embryos whose mothers had received a diet containing 8 p.p.m. 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

<i>Treatment</i>	<i>Number of fertile eggs</i>	<i>Hatch %</i>
Control	409	72.3
Selenium	509	49.6
Selenium + arsenic	419	69.2

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 (1934 a), Jull (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

Table 30

<i>Breed or cross</i>	<i>First laying year</i>		<i>Second laying year</i>	
	<i>No. of eggs</i>	<i>Fertile eggs hatched %</i>	<i>No. of eggs</i>	<i>Fertile eggs hatched %</i>
Rhode Island Red	931	76.0 \pm 1.40	472	69.5 \pm 2.12
Barnevelder	796	61.4 \pm 1.73	144	50.7 \pm 4.17
White Leghorn	868	60.8 \pm 1.66	47	40.4 \pm 7.16
Wh. Leghn. x R.I.R.	713	60.6 \pm 1.83	480	57.5 \pm 2.26
Wh. Leghn. x Barnev.	212	55.2 \pm 3.41	80	52.5 \pm 5.53
R.I.R. x Barnev.	371	54.4 \pm 2.59	275	53.1 \pm 3.01
Total	3891	63.6 \pm 0.77	1498	59.0 \pm 1.27

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 31

<i>Number of females</i>			<i>2nd year</i>	<i>3rd year</i>	<i>4th year</i>	<i>5th year</i>
I	633	Mean hatchability %	61.4 \pm 0.09	53.2 \pm 0.07		
		Coefficient of variation	34.8 \pm 1.10	46.3 \pm 0.07		
II	219	Mean hatchability %	62.1 \pm 1.22	54.8 \pm 1.35	46.3 \pm 0.18	
		Coefficient of variation	34.9 \pm 1.85	44.0 \pm 1.97	54.8 \pm 3.29	
III	85	Mean hatchability %	62.0 \pm 2.37	59.0 \pm 2.33	57.9 \pm 2.56	46.5 \pm 2.89
		Coefficient of variation	34.4 \pm 3.01	35.6 \pm 3.13	40.9 \pm 3.62	57.2 \pm 5.65

Table 32

Age in years	Number of hens	No. of eggs set	Fertile eggs hatched %
2	159	5892	65.8
3	99	3408	58.5
4	84	2292	60.1
5	60	1097	68.2
6	39	707	74.0
7	11	220	70.0
8	3	43	81.5

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 in 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), *Tomhave* (1956), *Meirelles de Miranda* (1956) and *Baranovskaja* (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. *Baranovskaja* 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 *Tur* (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

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 ± 0.095 and -0.208 ± 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* (1934 a) 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 ± 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 ± 0.087 , Rhode Island Red pullets 0.248 ± 0.086 , White Leghorn hens -0.209 ± 0.064 , and Rhode Island Red hens 0.031 ± 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

		Hatchability %
White Leghorn	pausing pullets	72.48 ± 1.30
	non-pausing pullets	66.37 ± 1.90
	Difference	6.11 ± 2.30
Rhode Island Red	pausing pullets	66.15 ± 2.08
	non-pausing pullets	54.34 ± 1.87
	Difference	11.81 ± 2.79

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

Breed	Mean current egg production per pen of group showing hatchability above mean per cent hatchability of the females of each pen	Mean current egg production per pen of group showing hatchability below mean per cent hatchability of the females of each pen	Difference
Barred Plymouth Rocks	23.5 ± 1.0	21.7 ± 0.9	1.8 ± 1.3
Rhode Island Reds	25.0 ± 0.4	23.6 ± 0.4	1.4 ± 0.6
White Leghorns	25.9 ± 0.4	24.4 ± 0.4	1.5 ± 0.6

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 Gunns* (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 35

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

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 ;

$(C+D) - (A+B) = 2.95 \pm 0.87$; 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.

Table 36

Group	Hours of laying	Number of fertile eggs	Embryonic mortality %
A	To 9 a.m.	3103	32.00 \pm 0.83
B	9:05 a.m. to 12 m.	5042	33.71 \pm 0.67
C	12:05 p.m. to 2 p.m.	2221	36.69 \pm 1.02
D	After 2 p.m.	2362	35.14 \pm 0.98

Results very similar to those of *Hutt and Pilkey* have been reported by *Pritsker* (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. *Pritsker* 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

Season	Hours of laying	Total no. of eggs	Infertile %	Mortality during incubation days in %			Fertile eggs hatched %
				1-6	7-14	15-21	
March and April	To 10 a.m.	1385	4.7	2.8	2.5	8.0	86.7
	10—12	1385	5.2	1.8	2.9	7.5	87.8
	12— 2	1386	5.2	2.9	2.7	13.1	81.3
	2— 4	1367	5.1	2.4	2.3	14.0	81.3
August	To 10 a.m.	923	5.7	2.5	2.1	5.8	89.6
	10—12	873	7.1	2.3	1.0	7.3	89.4
	12— 2	915	3.5	2.1	1.6	5.8	90.5
	2— 4	736	4.1	2.2	2.0	4.2	91.6

Other investigations failed to yield results similar to those recorded by *Hutt and Pilkey* and by *Pritsker*. *Nicolaides* (1933) found a mean embryonic mortality for afternoon eggs of 27.87 ± 5.87 percent and for morning eggs of 22.42 ± 3.88 percent, with a difference of 5.45 ± 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 38

<i>Season of laying</i>	<i>Time of day of laying</i>	<i>Number of eggs set</i>	<i>Infertile %</i>	<i>Fertile eggs hatched %</i>
January 15 to February 7	Before 9 a.m.	605	22.0	76.9
	9 a.m. to 12 m.	382	25.9	72.8
	12 m. to 2 p.m.	432	22.7	79.4
	After 2 p.m.	180	28.9	76.6
February 8 to February 28	Before 9 a.m.	775	15.1	79.9
	9 a.m. to 12 m.	448	18.5	80.8
	12 m. to 2 p.m.	485	17.9	82.9
	After 2 p.m.	225	15.6	76.9
March 1 to March 21	Before 9 a.m.	753	15.7	69.4
	9 a.m. to 12 m.	509	17.5	72.1
	12 m. to 2 p.m.	447	16.1	77.3
	After 2 p.m.	192	20.3	75.2

Table 39

<i>Date set</i>	<i>Hatchability of fertile eggs in %</i>			
	<i>Eggs laid before 9 a.m.</i>	<i>Eggs laid from 9 a.m. to 12 m.</i>	<i>Eggs laid from 12 m. to 2 p.m.</i>	<i>Eggs laid after 2 p.m.</i>
January 15 to March 18, 1932	72.3	71.4	75.7	77.3
January 13 to March 4, 1933	74.2	73.3	76.6	76.8

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

Year	Morning eggs		Afternoon eggs		Difference in favor of afternoon eggs %
	Number of eggs set	Fertile eggs hatched %	Number of eggs set	Fertile eggs hatched %	
1931	3472	75.7	1961	78.8	3.1
1932	4108	74.5	2326	76.5	2.0
1933	2589	73.8	2383	76.7	2.9
1934	3204	68.0	2093	74.4	6.4

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 *Prütsker* 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 Gunns (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

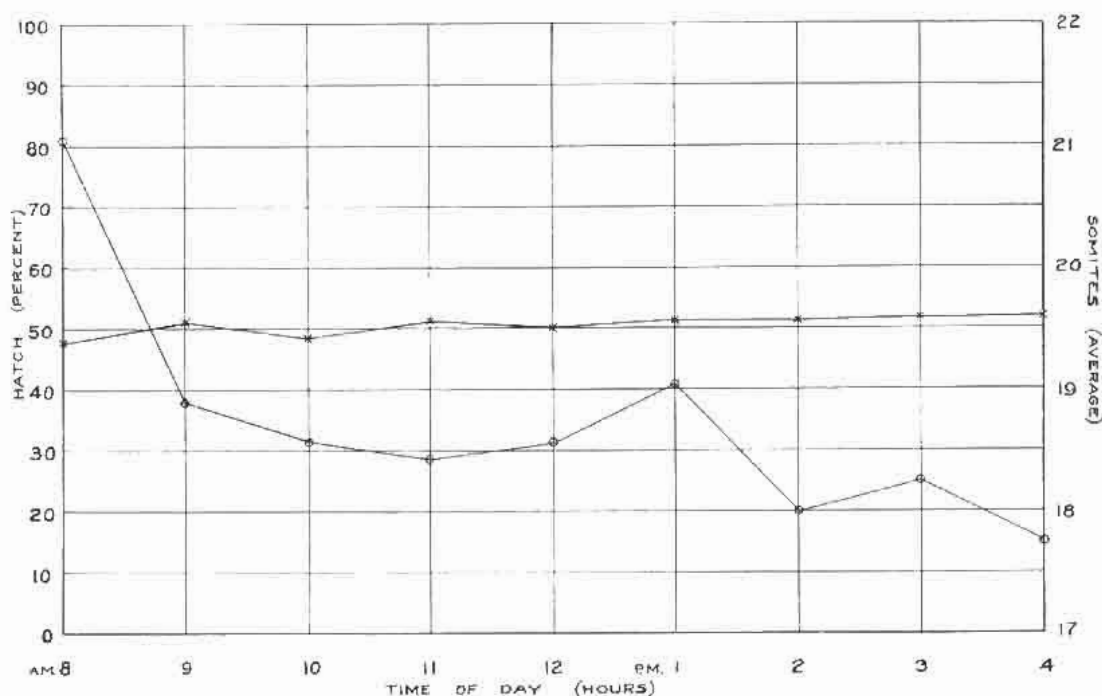


Figure 25

Relationship (o) between degree of development (number of somites) after 48 hours of incubation and time of the day when the eggs were laid; and relationship (x) between percentage hatchability and time of the day when the eggs were laid (From *McNally and Byerly, 1936*).

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 24 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.

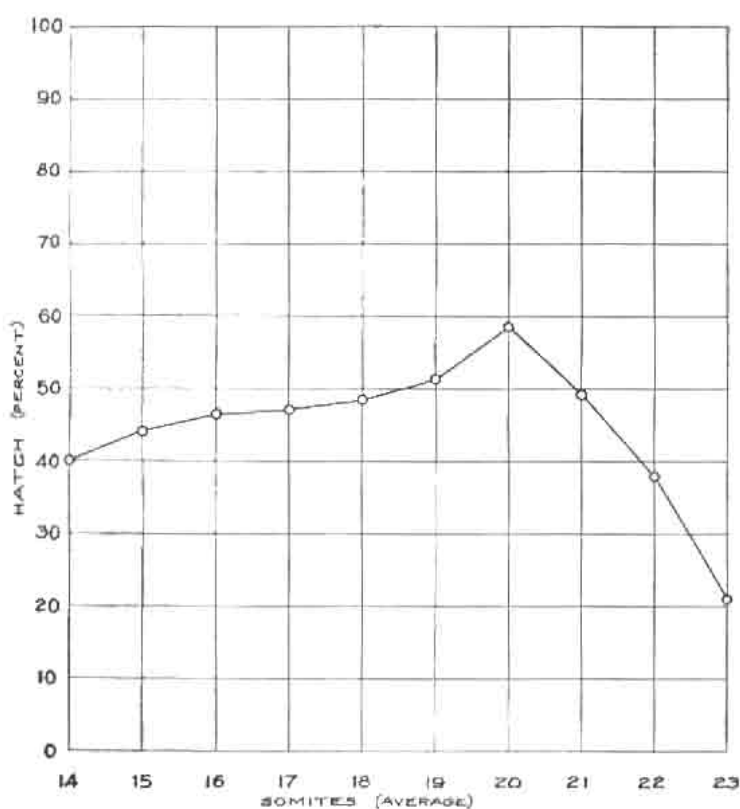


Figure 26

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 Gunns* (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

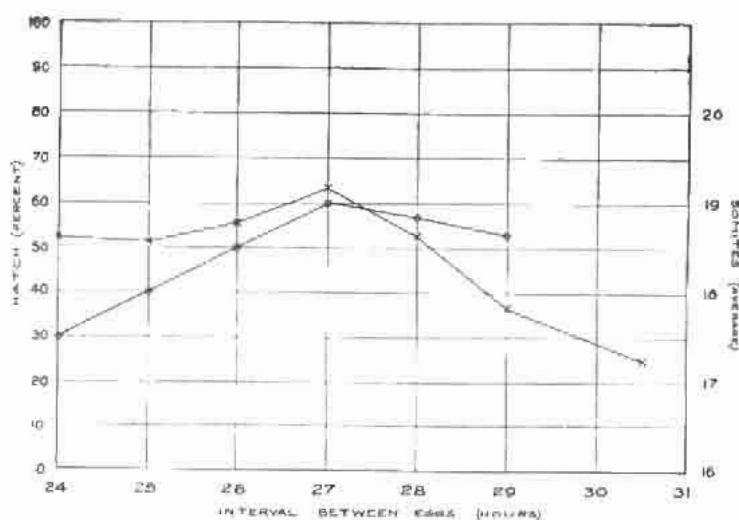


Figure 27

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 Gunns* (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 41

	Time interval in hours between successive eggs						
	24	25	26	27	28	29	30
Number of eggs in class	5	10	29	19	34	29	3
Mean somite number	6.0	7.4	7.7	7.6	9.0	8.9	10

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 Gunns* (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

<i>Time between clutches (hours)</i>	<i>Number of birds</i>	<i>Hatchability of fertile eggs in %</i>
41.5	5	59.5
44.5	15	61.9
47.5	8	40.9
50.5	8	47.3
53.5	7	56.9
56.5	2	35.5
65.5	2	27.8

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

<i>Author</i>	<i>Material</i>	<i>Coefficient of correlation between fertility and hatchability</i>
<i>Pearl and Surface</i> (1909)	Barred Plymouth Rock	
	110 pullets (1908)	0.417 ± 0.053
	146 pullets and hens (1909)	0.142 ± 0.055
<i>Hays and Sanborn</i> (1924)	Rhode Island Red	
	758 pullets	0.067 ± 0.024
<i>Knox</i> (1926-1927)	White Plymouth Rock	
	92 pullets	0.59 ± 0.06
<i>Jull</i> (1927-1928)	Barred Plymouth Rock	0.276 ± 0.078
	Rhode Island Red	0.025 ± 0.048
	White Leghorn	0.012 ± 0.040
<i>Hyre and Hall</i> (1932)	White Leghorn	
	801 hens	0.056 ± 0.024
<i>Munro and Kosin</i> (1945)	Barred Plymouth Rock	0.332 ¹
	White Leghorn	0.265 ²
<i>Hays</i> (1951 b)	Rhode Island Red	
	848 hens	0.202 ± 0.022

¹Significant at 1% level; ²Significant at 5% level.

In a small group of Brown Leghorn fowl *Blyth* (1945) 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 Gunns*, 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									
			Number of days after removal of male from females						
			1-5	6-10	11-15	16-20	21-25	26-30	31-35
Eggs warmed to 100°F. for one hour daily dur- ing storage for seven days at 55°-60°F.	a	Number fertile eggs	24	24	12	7	1	7	3
		Hatched %	58.3	75.0	50.0	14.3	0	0	0
	b	Number fertile eggs	104	84	53	12	2	1	—
		Hatched %	69.2	63.1	77.4	33.3	0	0	—
Eggs set daily		Number fertile eggs	66	63	31	7	—	10	3
		Hatched %	78.3	71.4	32.3	0	—	0	0
Eggs set after seven days storage at 55°-60° F.	a	Number fertile eggs	60	50	42	9	6	2	5
		Hatched %	78.3	68.0	23.8	0	0	0	0
	b	Number fertile eggs	104	81	58	9	1	—	—
		Hatched %	49.0	54.3	60.3	77.8	0	—	—

Table 45

<i>Age of sperm in relation to mean age at death of those embryos which died during the incubation period.</i>							
Number of days after removal of cocks	1-5	6-10	11-15	16-20	21-25	26-30	31-35
Mean age at death	12.4	11.0	5.5	3.5	1.6	1.0	1.0

tures of such embryos. *Dharmarajan* 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 *Dharmarajan* 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 pre-oviposital 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

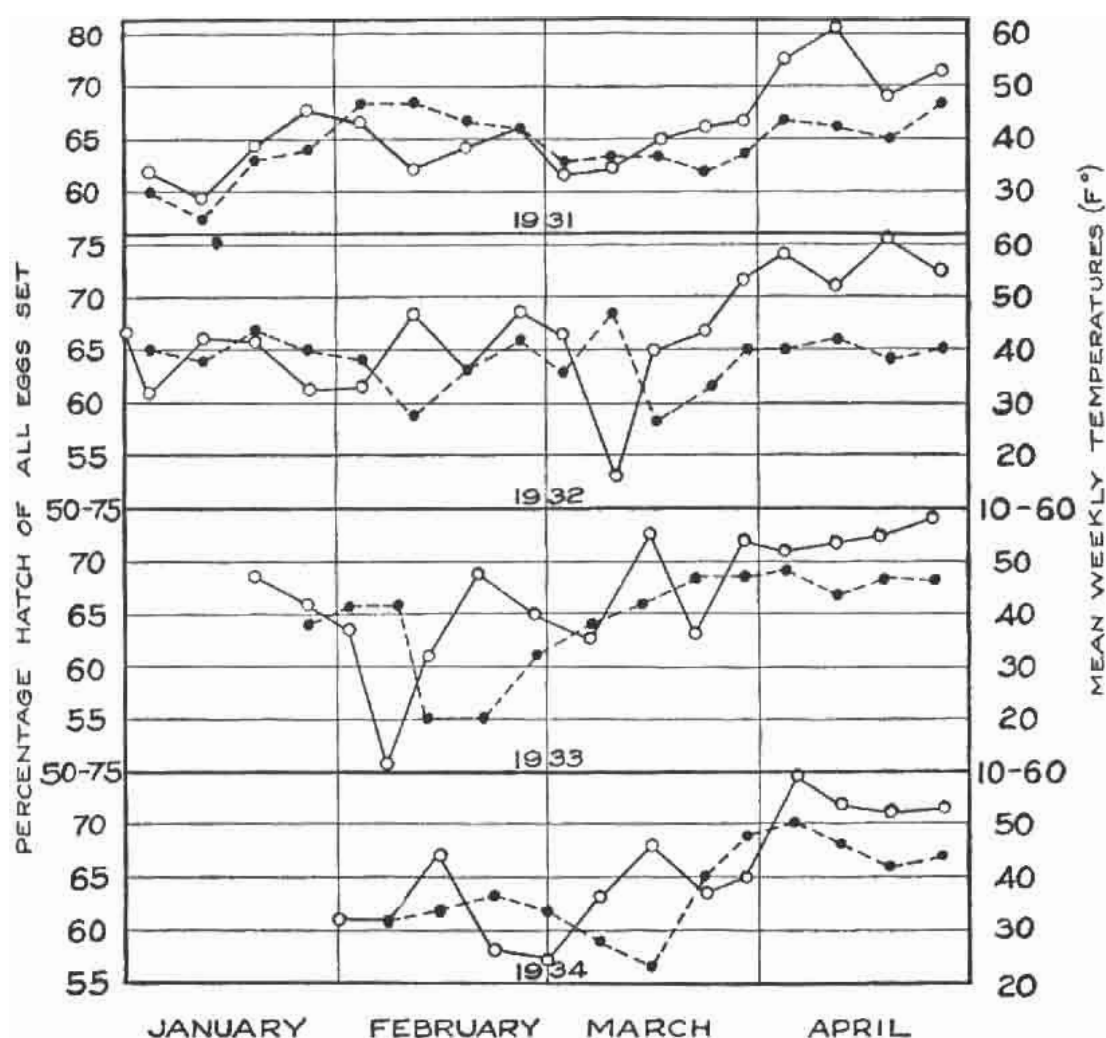


Figure 28

The effect of sudden drops in outside temperature on hatching results. Data of a commercial hatchery during four years. Hatchability is based on the number of all eggs incubated (From Funk, 1934 a). Solid lines temperature; broken lines hatchability.

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), *Mussehl and Bancroft* (1924-1925), *Warren* (1934) *Funk* (1934 a) 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

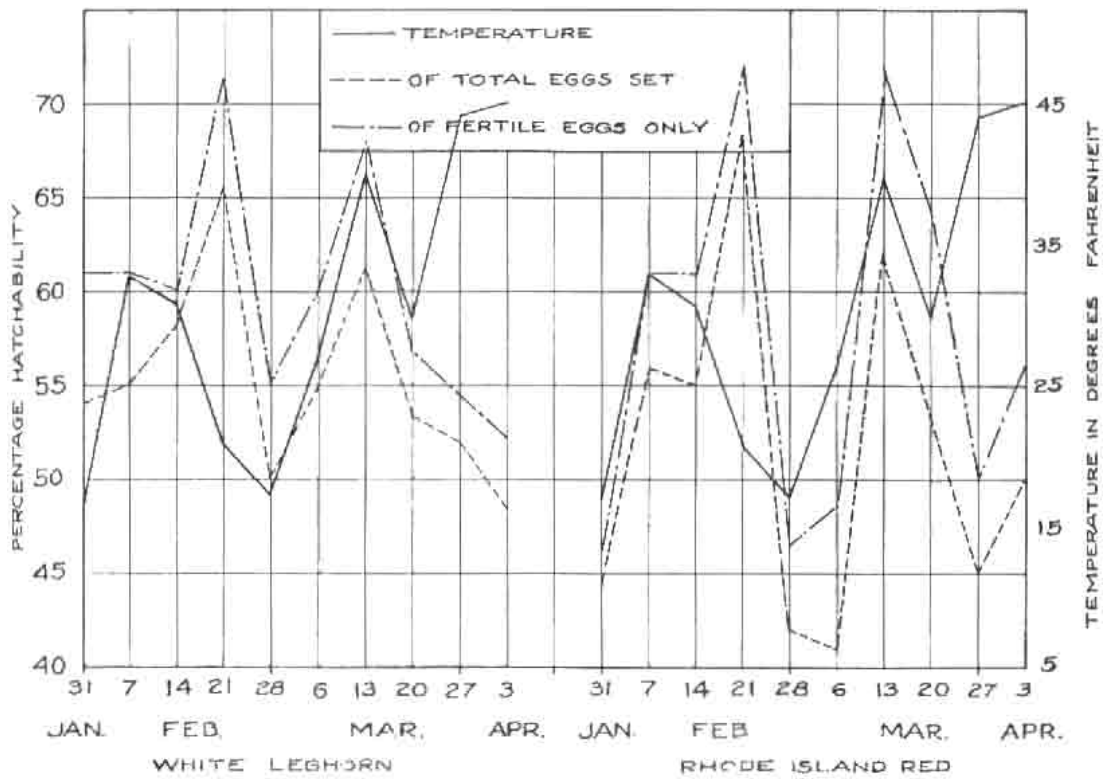


Figure 29

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 Storrs 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 cloacae and three coeca. The V-shaped colon opened into the two cloacae. 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:

<i>Fertile eggs</i>	<i>Mortality during incubation days in %</i>				<i>Hatched</i>
	1-6	7-13	14-16	17-22	
23	17.4	60.9	4.3	17.4	0

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:

<i>Fertile eggs</i>	<i>Mortality during incubation days in %</i>				<i>Hatched</i>
	1-6	7-13	14-16	17-22	
36	27.8	8.3	11.1	27.8	25.0

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 F_1 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 (♂ 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 ♀ 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, Guckler 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 Pit Game male all the F_1 offspring were colored, as expected. But, when some of the F_1 males were crossed each to his own mother, abnormal segregation with regard to plumage color occurred in two sibships. One of these cocks (♂ 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 ♂ 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 46

Mate	Geno- type	OFFSPRING				
		Actual			Expected	
		Colored (C)	White (cc)	Total	Colored	White
Daughter 258	Cc	18	5	23	17.3	5.7
Half-sister 44	Cc	29	5	34	25.5	8.5
Niece 199	cc	10	10	20	10.0	10.0
Total		57	20	77	52.8	24.2
Mother 8	cc	19	8	27	13.5	13.5
Aunt 12	cc	17	8	25	12.5	12.5
Aunt 14	cc	2	1	3	1.5	1.5
Cousin 505	cc	9	5	14	7.0	7.0
Cousin 519	cc	1	2	3	1.5	1.5
Cousin 523	cc	10	8	18	9.0	9.0
Total		58	32	90	45.0	45.0

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.

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 47

Mating	Number of fertile eggs	Mortality during incubation %			Hatched %
		1-6	7-16	17-22	
Creeper x normal	1136	6.9	4.6	19.6	68.9
Creeper x Creeper (same lines)	1444	28.5	4.4	26.7	40.4
Creeper x Creeper (different lines)	1714	23.3	3.6	16.6	56.6

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).

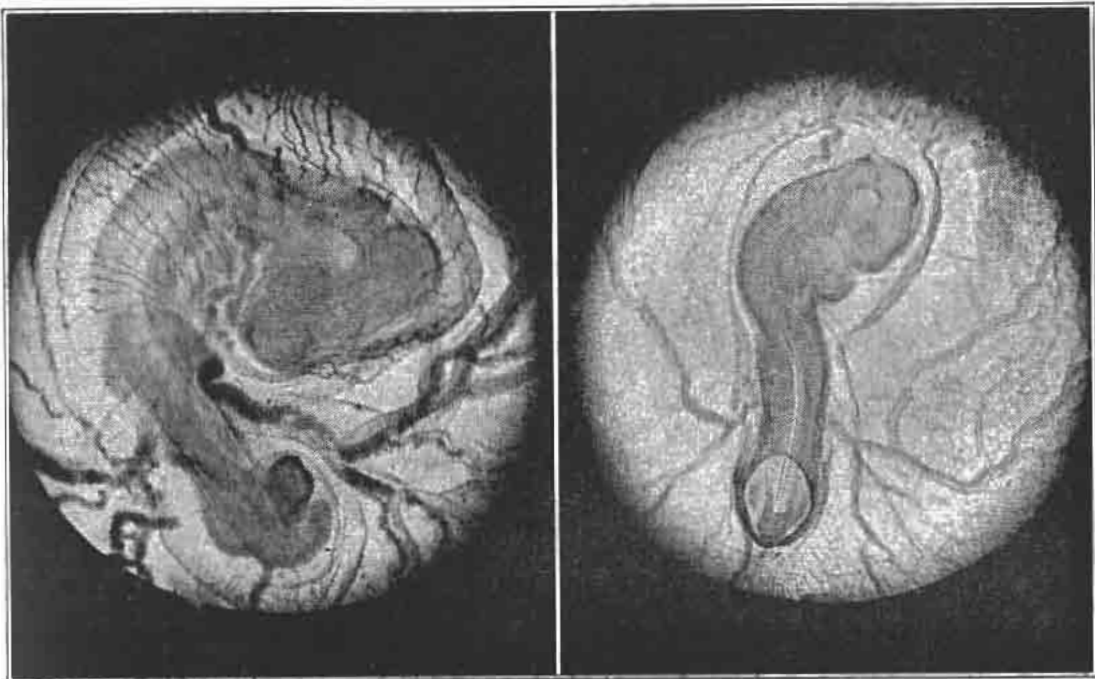


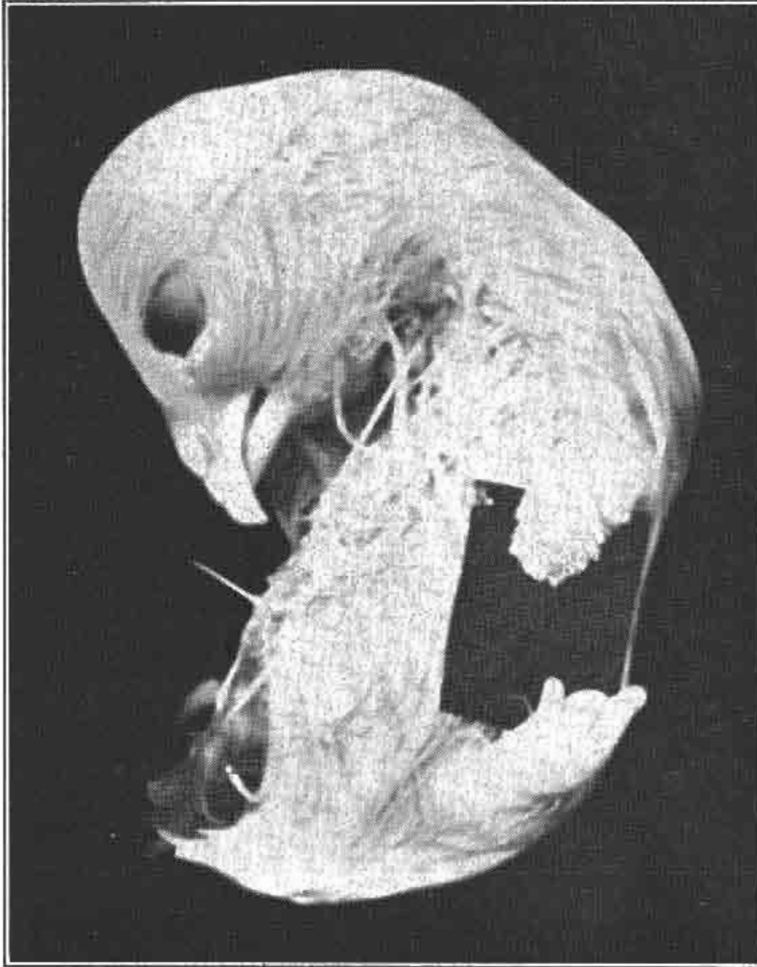
Figure 30

A normal (left) and a homozygous Creeper (right) embryo after 72 hours of incubation.

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

Table 48

<i>Mating</i>	<i>Hatched</i>		<i>Dead in shell</i>		<i>Total</i>	
	<i>Creeper</i>	<i>Normal</i>	<i>Creeper</i>	<i>Normal</i>	<i>Creeper</i>	<i>Normal</i>
Creeper outcross with normal						
Actual	910	1122	766	539	1676	1661
Expected	1016	1016	652.5	652.5	1668.5	1668.5
Creeper inter se						
Actual	412	227	363	161	775	388
Expected	426	213	349.3	174.7	775.3	387.7

**Figure 31**

A homozygous Creeper embryo at the age of 19 days. Note that the head has an abnormal shape, the eyelids are rudimentary, and the extremities show a condition known as phocomelia.

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 depots). 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.

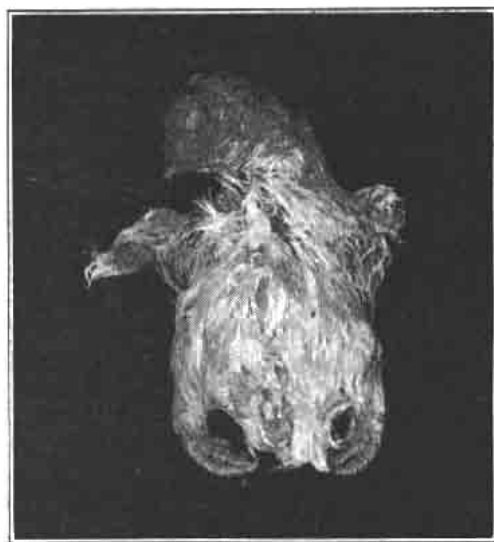


Figure 32

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

Table 49

Group	Number of fertile eggs	Mortality during incubation %			Hatched %	Deformed embryos %
		1-6	7-16	17-22		
I	1135	3.5	5.0	36.2	55.3	23.1
II	339	5.6	5.9	19.2	69.3	0

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 *Upp* (1934 and *Upp 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

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

Table 50

<i>Female No.</i>	<i>Normal upper mandible</i>				<i>Abnormal upper mandible</i>			
	<i>Males</i>	<i>Females</i>	<i>Sex un- known</i>	<i>Total</i>	<i>Males</i>	<i>Females</i>	<i>Sex un- known</i>	<i>Total</i>
I 13	14	17	0	31	6	1	1	8
K 12	1	4	0	5	1	1	0	2
K 36	5	14	0	19	3	2	2	7
K 46	3	1	3	7	1	0	1	2
K 68	28	18	1	47	11	8	2	21
K 91	5	4	3	12	2	0	2	4
K 93	5	6	2	13	1	2	0	3
K 100	17	20	2	39	4	6	1	11
Total	78	84	11	173	29	20	9	58

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

Table 51

<i>Group</i>	<i>Number of fertile eggs</i>	<i>Embryonic mortality in percent</i>			<i>Hatched %</i>
		<i>1-7 days</i>	<i>8-14 days</i>	<i>15-21 days</i>	
I	245	5.0	9.0	37.1	49.0
II	67	13.4	9.0	14.9	62.7

(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 polydactylism, involving both pairs of extremities, a marked reduction in length of the proximal long bones of legs and wings, ectopia viscerum 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.



Figure 33

Lethal embryo with deformed maxillae of upper mandible from White Leghorn stock. Age 21 days (From *Asmundson*, 1936).

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, 1941 a). This mutation produces a variable reduction in



Figure 34

A 17 day embryo with lethal polydactyly (From Cole, 1942).

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

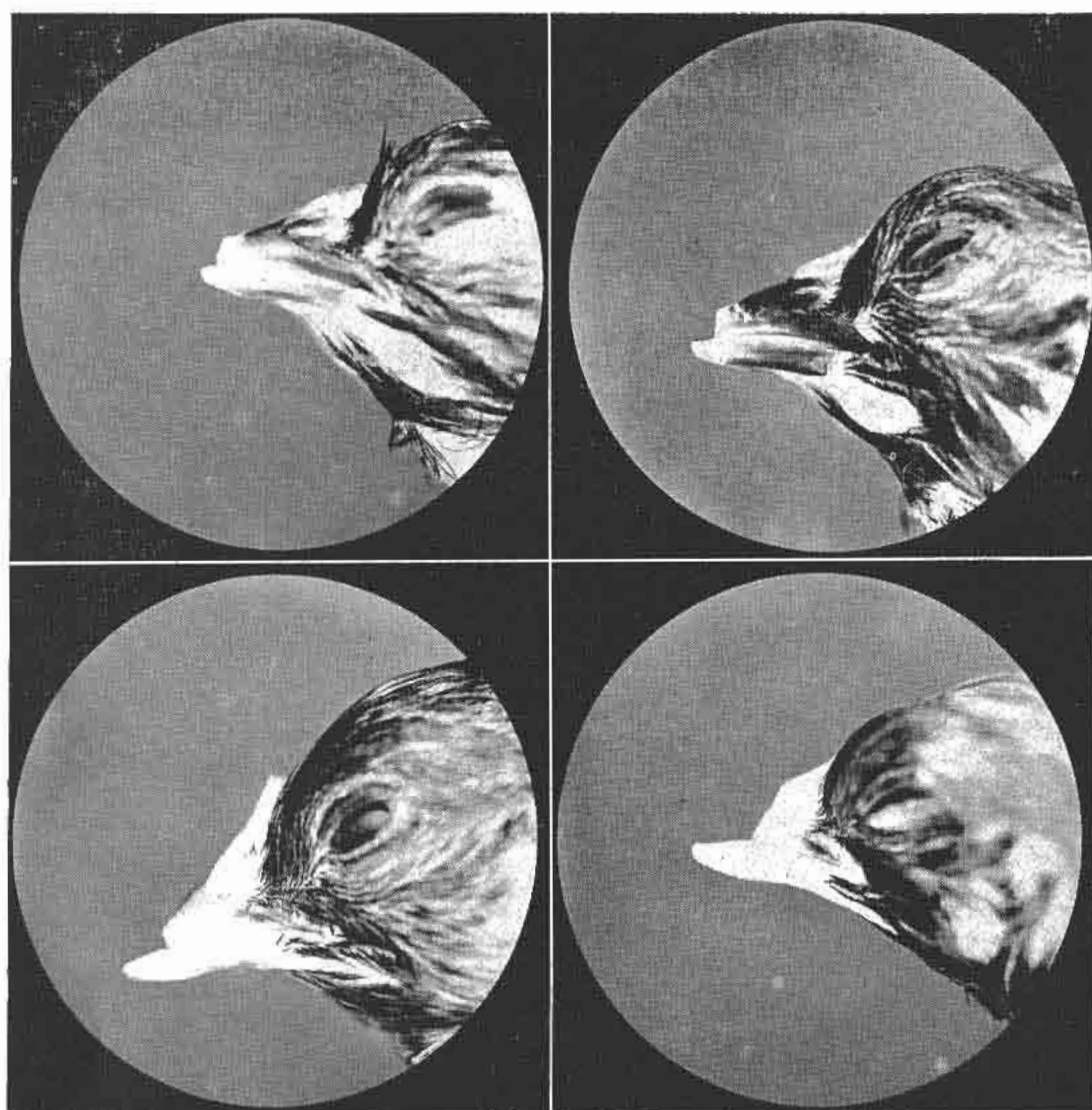


Figure 35

Four different degrees in expression of the "short upper beak" lethal in late embryos.

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 52

Type of mating	Number of fertile eggs	Embryo mortality during incubation days in %			Hatched		Dead embryos (19-22 days)	
		1-6	7-18	19-22	Normal %	"Short upper beak" %	Normal %	"Short upper beak" %
Normal ♀♀ x heterozygous ♂	675	5.0	4.6	14.5	75.9	0	14.5	0
Heterozygous inter se	742	7.1	5.0	33.3	51.6	3.0	13.9	19.4
Normal ♀♀ x homozygous ♂	73	9.6	5.6	6.8	78.1	0	6.8	0
Heterozygous ♀♀ x homozygous ♂	294	6.5	8.5	46.3	34.1	5.4	11.2	35.0

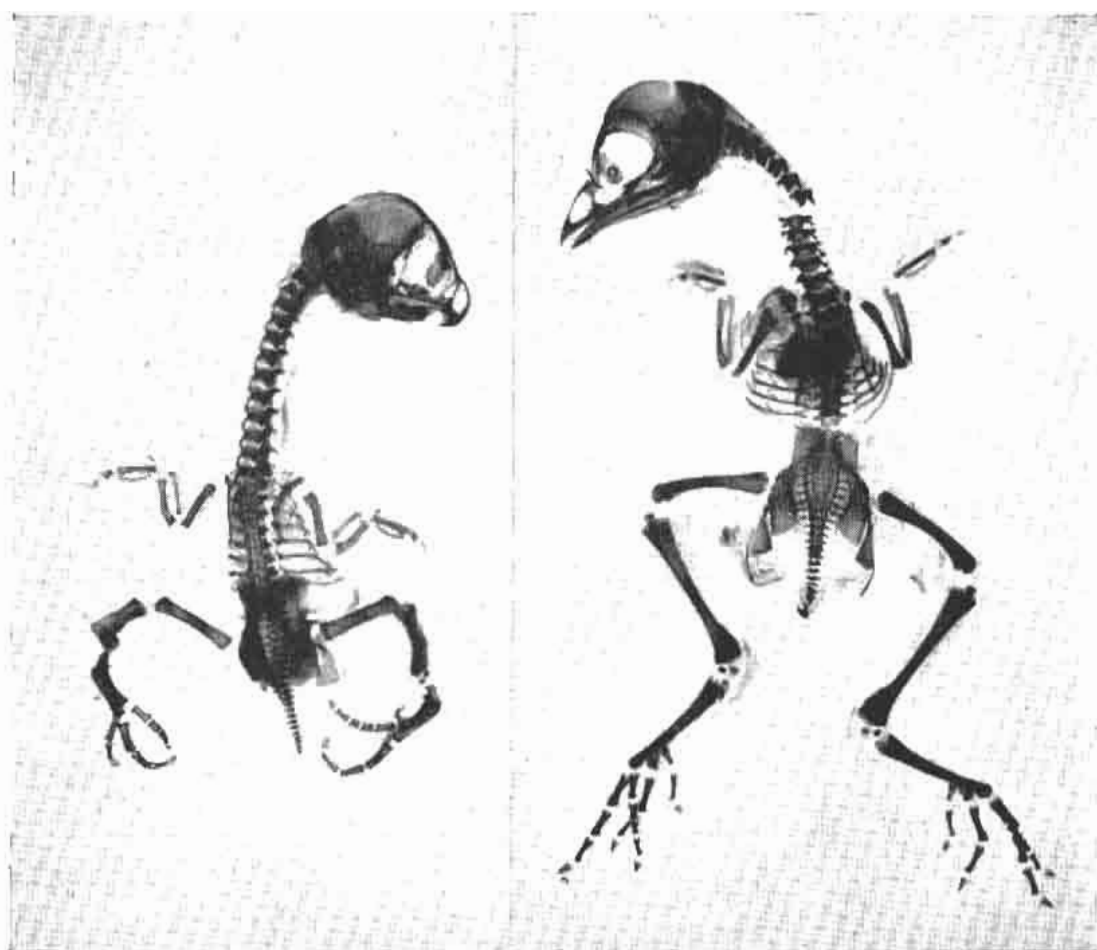


Figure 36

The skeleton of a chondrodystrophic embryo of the extreme type (left) and of a normal embryo (right) after 21 days of incubation. (From *Lamoreux, 1942*).

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

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

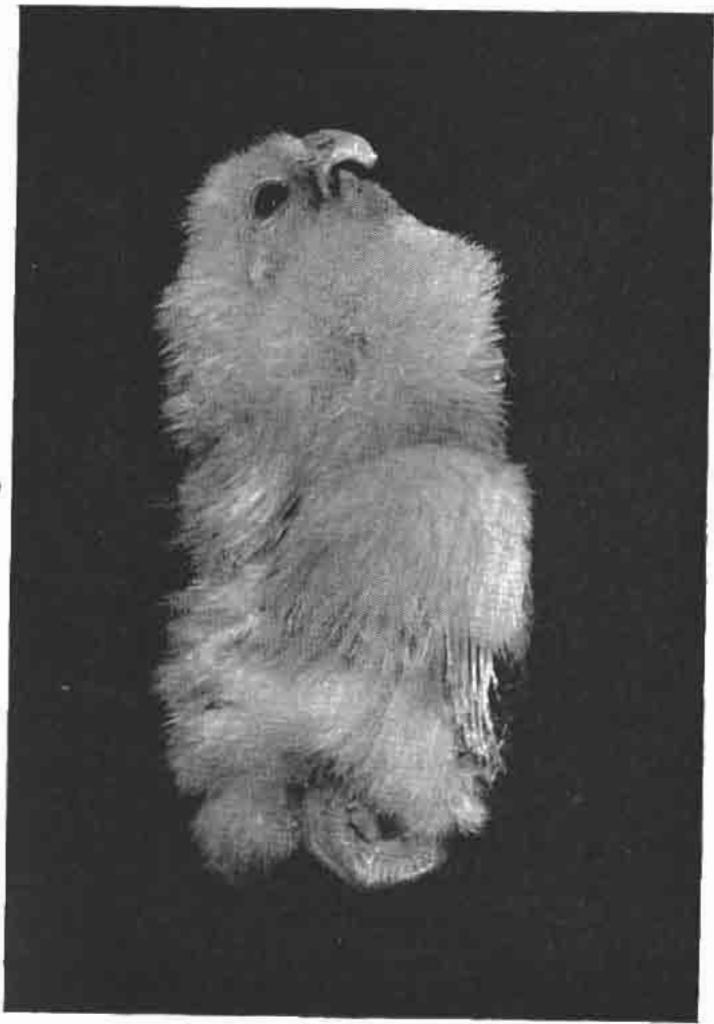


Figure 37
Chondrodystrophy of the extreme type in a newly-hatched chick (From Lamoreux, 1942).

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-

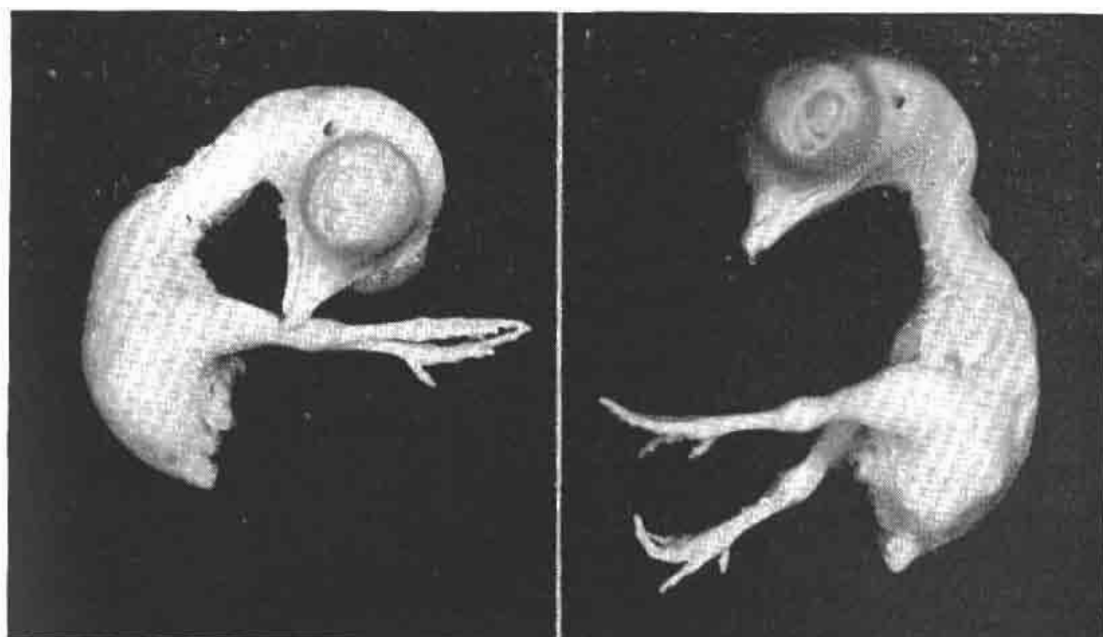


Figure 39

A wingless embryo (left) and one with wing vestiges (right). Courtesy of Dr. Edgar Zwilling.

ties. 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 syndactylous, 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-

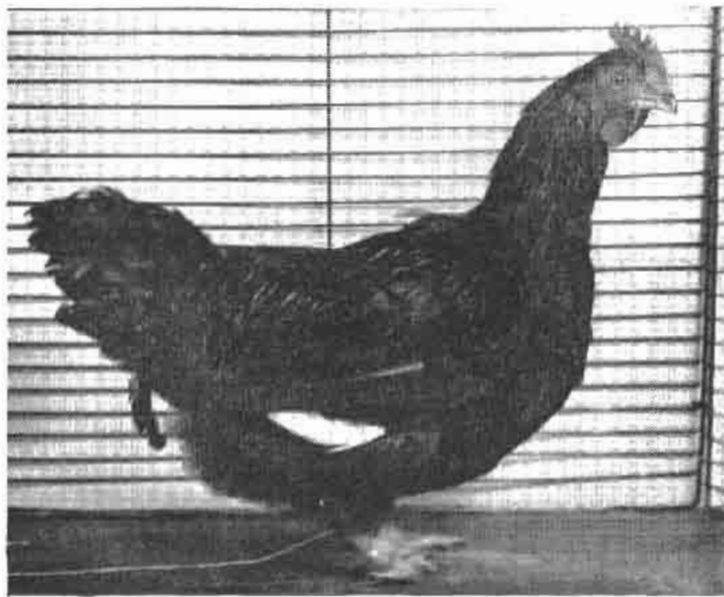


Figure 40
An adult Rhode Island Red male with hereditary micromelia.

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, Hammers 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.

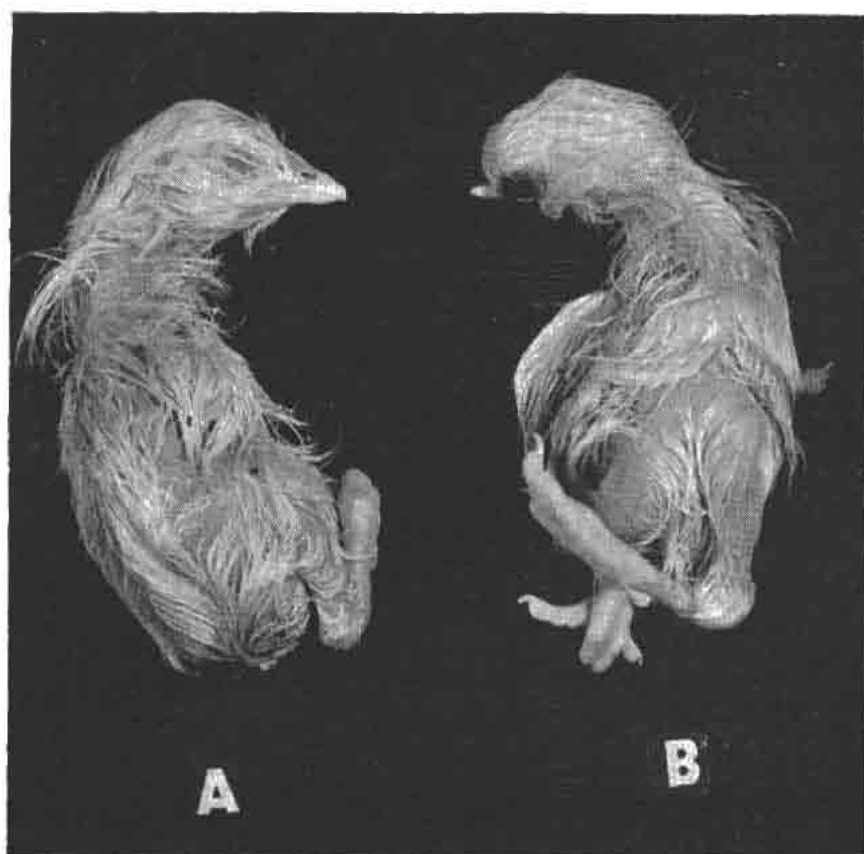


Figure 41

Normal embryo (left) and one with hereditary abnormality of maxilla and mandible (right), both 21 days of incubation (From *Marble, Harper and Hammers, 1944*).

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.

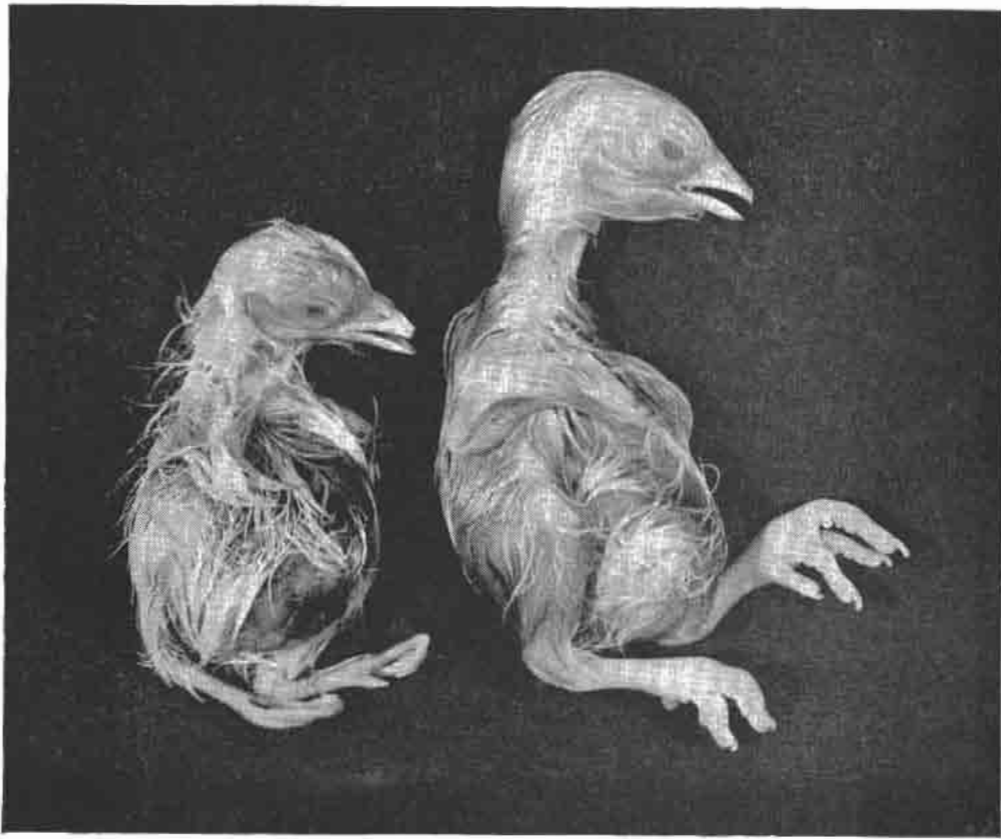


Figure 42

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 polydactylism 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).

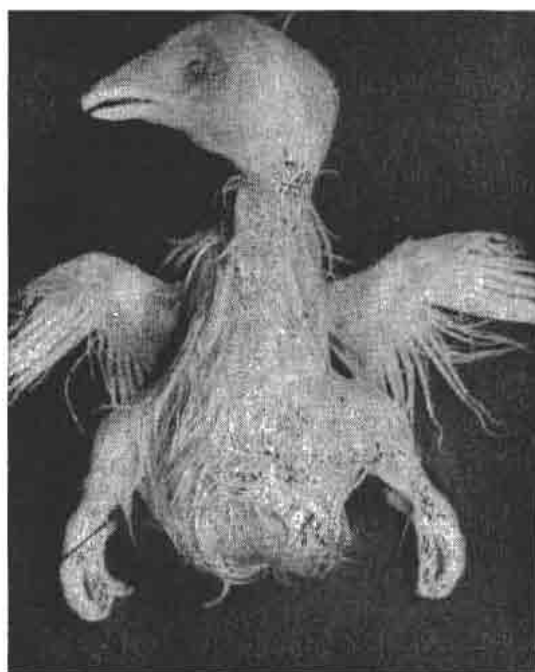


Figure 44

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 Gunns* (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

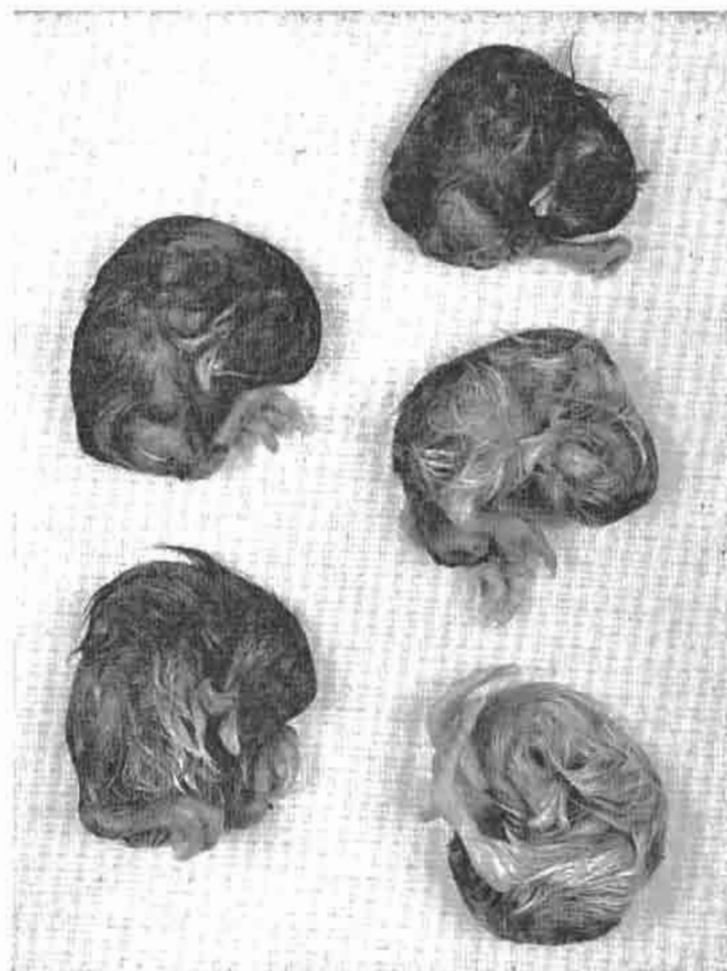


Figure 45

Embryos with varying expressions of the "curled beak" mutation
(Courtesy of *Brockhuizen and van Albada*)

helped out of the shell, and one such chick lived to the age of $7\frac{1}{2}$ 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

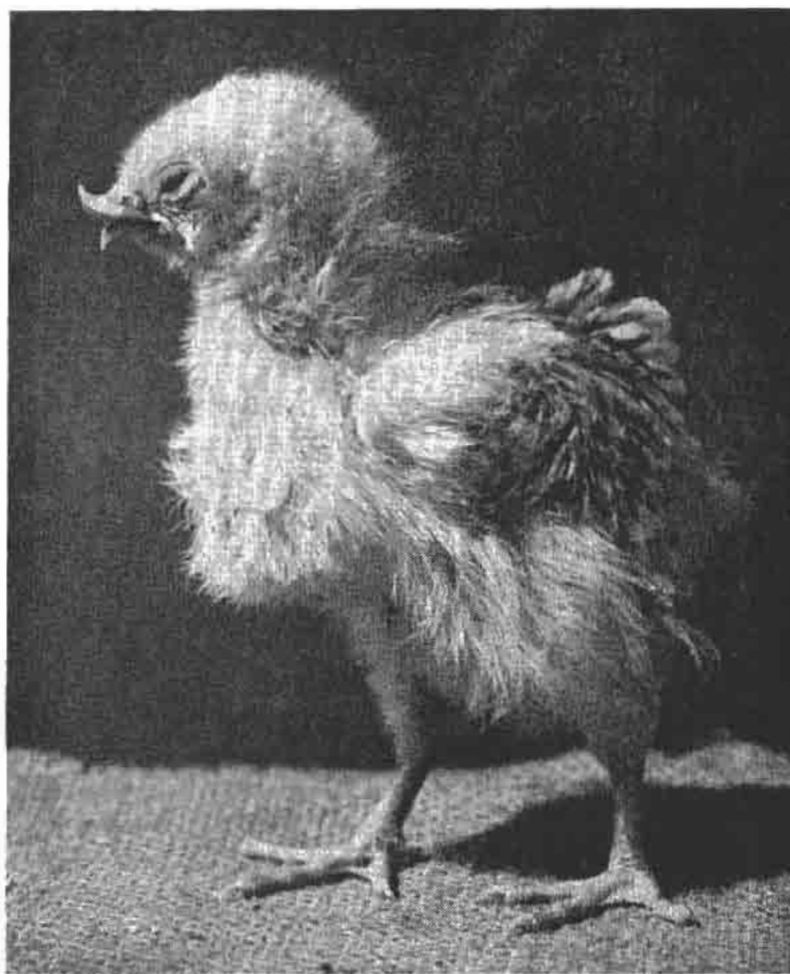


Figure 46

A "curled beak" chick that was raised to the age of 7½ weeks
(Courtesy of Broekhuizen and van Albada)

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 diplopodia 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-



Figure 47

Black Minorca embryo with diplopodia.

tions are synophthalmia and cyclopia (Fig. 48). The perocephaly mutant was found at the Storrs Agricultural Experiment Station in F_2 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 homozygotes 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-

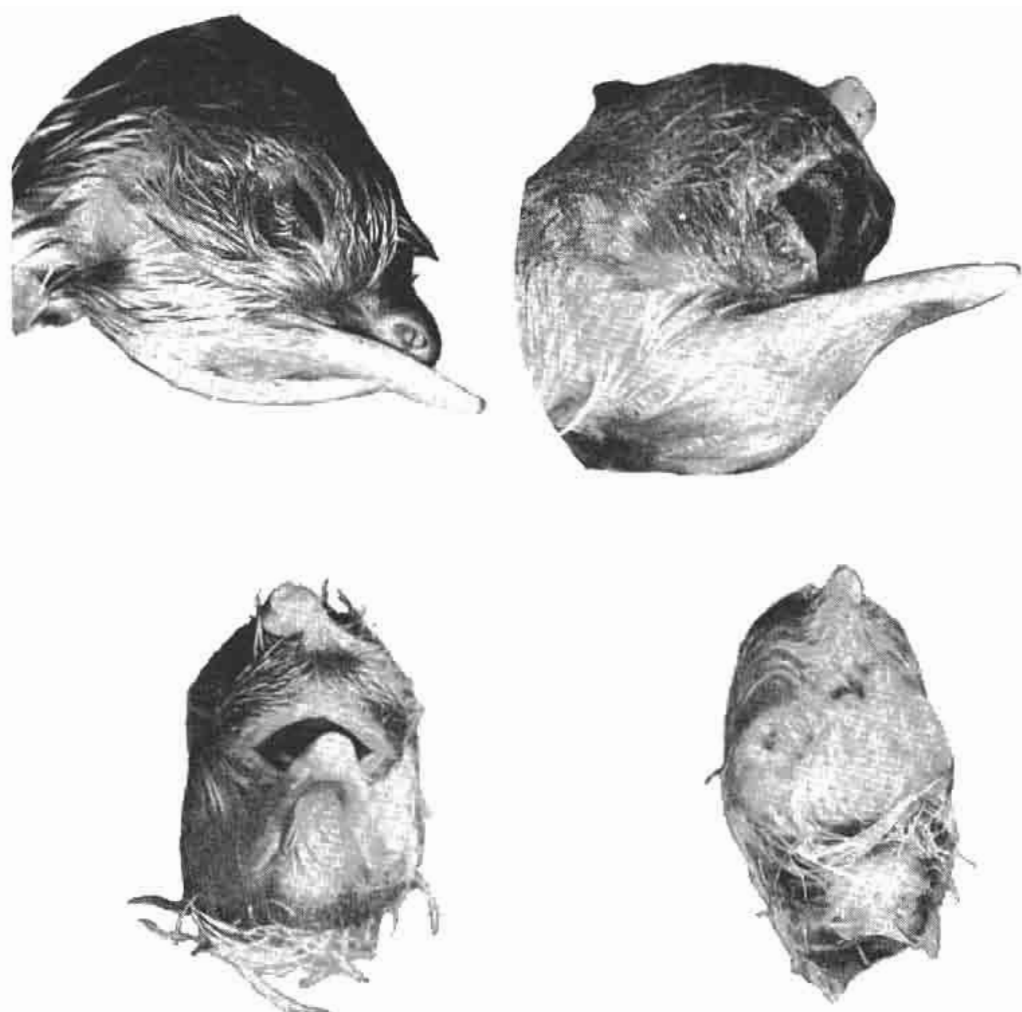


Figure 48

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.

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.

A brief report by *Abbott, Taylor and Abplanalp* (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 *Cole* which has already been discussed. Hence the new lethal is designated as talpid² (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 talpid² 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,

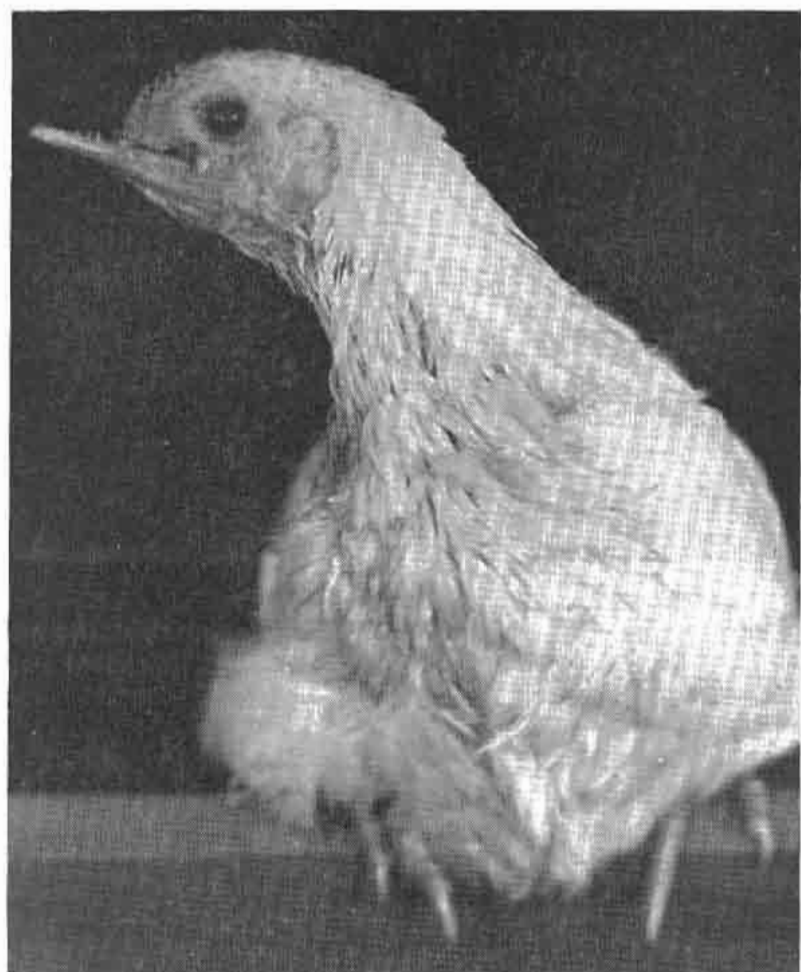


Figure 49

A blind perocephalic 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 ta^2 gene.

A twenty-first lethal of fowl was discovered by *Rosenblatt, Kreutziger and Taylor* (1959), also in the White Leghorn stock of the University

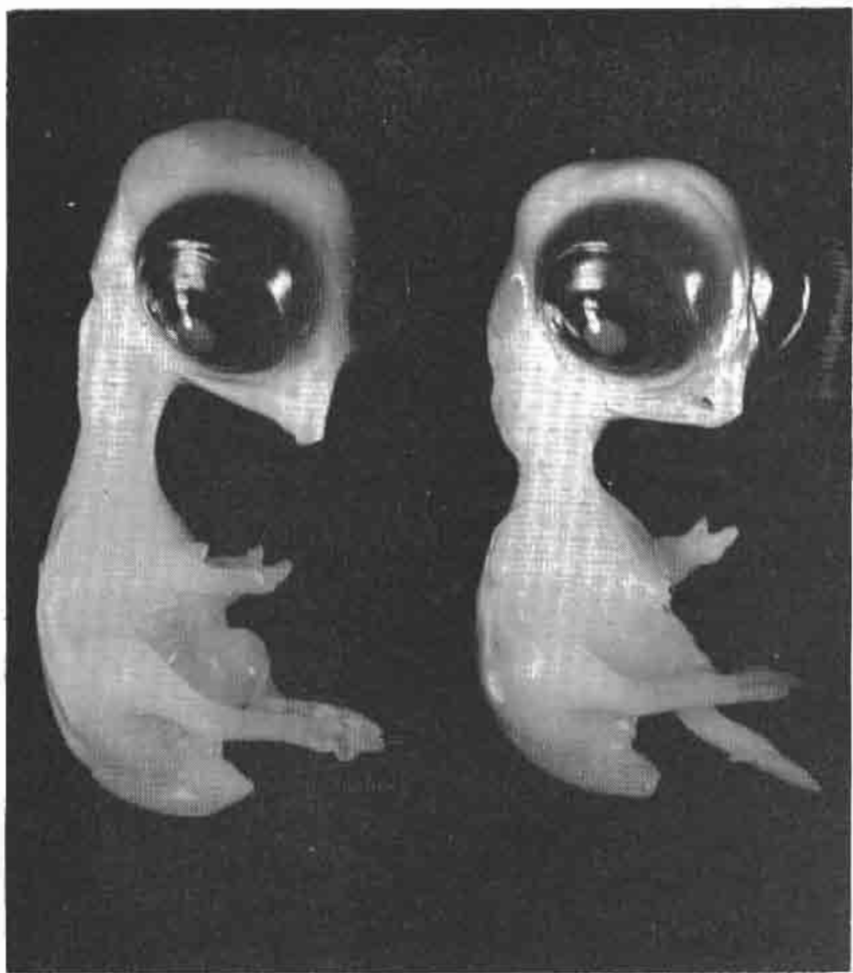


Figure 50

Embryo homozygous for "short neck" lethal mutation right; normal sib left; both 8½ days old. Note short neck and beak of lethal embryo.

of California. It is represented by yet another form of polydactylism. 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 *Maw* 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 ♀ x Rhode Island Red ♂ 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 54

<i>Type of mating according to feathering</i>			<i>Number of fertile eggs</i>	<i>Mortality during incubation periods</i>			<i>Hatch %</i>	<i>Phenotype of embryos</i>
<i>No.</i>	<i>Females</i>	<i>Males</i>		<i>1-6</i>	<i>7-13</i>	<i>14-22</i>		
1	rapid	rapid	134	2	21	16	61	all rapid
2	rapid and slow	slow	577	7	25	23	45	all slow
3	slow	rapid	301	5	26	15	54	50% rapid, 50% slow

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-schkevitch* (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 Cooney* (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 bred 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* (1944). 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 F_2 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), *Shuklee 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 F_2 embryos from this cross none survived the seventh day of incubation. In a cross of domestic hens to an F_1 cock only 7 out of 51 fertile eggs produced chicks, and in a mating of one such backcross female to an F_1 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 (F_1 embryos) fertility and hatchability were satisfactory. The results of *inter se* matings between F_1 hybrids (F_2 embryos), obtained from reciprocal crosses, and of backcrosses of F_1 animals to *Gallus gallus* are summarized in Table 55. None of the more than 1200 F_2 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 F_2 , but a few chicks hatched. Experiments by Danforth (1958 and personal communication) produced similar results. In the cross of (domestic ♀ x sonnerati ♂) F_1 ♀ x (domestic ♀ x gallus ♂) F_1 ♂ 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 F_2 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 F_1) permits normal development and unimpaired viability, but that chromosomal segregation (in F_2) 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 F_1 animals seem to occur (*Deraniyagala* 1953, 1956), but little is known about their breeding behavior. *Newton* (1893-96) had reported them as sterile.

Table 55

Cross	Number of fertile eggs	Results of incubation
(<i>G. sonnerati</i> ♀ x <i>G. gallus</i> ♂) F_1 inter se	47	All dead by end of second week
(<i>G. gallus</i> ♀ x <i>G. sonnerati</i> ♂) F_1 inter se	1162	Principal period of mortality between 11th and 15th day. None hatched. Many malformed.
(<i>G. gallus</i> ♀ x <i>G. sonnerati</i> ♂) ♀ x <i>G. gallus</i> ♂	88	None hatched
One ♀ of preceding group x another <i>G. gallus</i> ♂	13	11 viable chicks
<i>G. gallus</i> ♀ x F_1 ♂ (<i>G. gallus</i> ♀ x <i>G. sonnerati</i> ♂)	116	5 viable chicks

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:

<i>Days of incubation</i>	<i>Number of dead embryos</i>	<i>Males %</i>
9-11	176	50.0 \pm 3.79
12-18	948	61.6 \pm 1.58
19-21	1539	40.9 \pm 1.26

The deviations from equality are highly significant in the last two groups ($\chi^2 = 25.88$ 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 56

Generation	Family IV		Family II		Family VIII		Family VII	
	Number of fertile eggs	Hatch %	Number of fertile eggs	Hatch %	Number of fertile eggs	Hatch %	Number of fertile eggs	Hatch %
P ₁	29	70.4	25	95.8	27	85.2	28	64.3
F ₁	50	56.0	220	60.0	383	51.4	214	49.5
F ₂	182	44.5	605	57.2	703	49.8	383	37.9
F ₃	294	29.6	286	45.8	94	19.1	107	40.2
F ₄	130	50.0	11	18.2				
F ₅	65	41.5						

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

Generation	Inbred families			Outbred stock	
	Number of families	Number of fertile eggs	Hatch %	Number of fertile eggs	Hatch %
P ₁	8	204	75.0	—	—
F ₁	8	1304	50.5	520	49.8
F ₂	7	2269	46.7	492	67.5
F ₃	5	932	34.3	768	60.8
F ₄	2	141	46.8	531	60.1
F ₅	1	65	41.5	742	59.2

Crosses 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 I₂ and family I₈ 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 F₂ 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

Family and type of mating	Number of fertile eggs	Hatch %
Inbreeding: $I_2 \text{ } \varnothing \varnothing \times \text{brother}$	174	47.4
$I_4 \text{ } \varnothing \varnothing \times \text{brother}$	140	53.0
Cross: $I_3 \text{ } \varnothing \varnothing \times I_4 \text{ } \sigma$	151	85.0
New inbreeding: $I_{24} F_1$		
mating a, brother-sister	245	69.0
" b, brother-sister	97	49.5
" b, half-brother-sister	87	49.4
" c, brother-sister	81	51.9
" c, half-brother-sister	103	56.3
" d, brother-sister	187	70.1
$I_{24} F_2$		
descendants of F_1 , a		
brother-sister	91	41.2
half-brother-sister	68	39.7
descendants of F_1 , d		
brother-sister	98	64.3
half-brother-sister	124	72.6
brother-sister	64	67.2
Inbreeding: $I_{24} F_3$		
$I_8 \text{ } \varnothing \varnothing \times \text{brother}$	136	56.3
$I_2 \text{ } \varnothing \varnothing \times \text{brother}$	174	47.4
Cross: $I_8 \text{ } \varnothing \varnothing \times I_2 \text{ } \sigma$	127	73.4
New inbreeding: $I_{82} F_1$	284	52.5
$I_{82} F_2$ mating a, brother-sister	55	41.8
" a, half-brother-sister	87	51.7
" b, brother-sister	106	30.4
" b, half-brother-sister	106	28.0
$I_{82} F_3$	198	39.4

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

Mating	Number of fertile eggs	Hatch %
$I_{24} \text{ } \varnothing \varnothing \times I_{82} \text{ } \sigma$		
mating a	268	63.1
mating b	168	55.4
$I_{82} \text{ } \varnothing \varnothing \times I_{24} \text{ } \sigma$	198	65.2

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), *Jull* (1928-1929 a and b; 1929-1930), *Dumon* (1931, 1938), *Dunkerly* (1931), the Northern Sub-Committee of the National Poultry Institute (1934), *Funk*

(1934 a), *Iecchi* (1936), *Bice and Tower* (1939), *Knox, Quinn and Godfrey* (1943), *Jeffrey* (1944), *Shoffner* (1948 a and b), *Bernier* (1947), *Wilson* (1948), *Düzgünes* (1950), *Bernier, Taylor and Gunns* (1951), *Hutt and Cole* (1952), *Wyatt* (1953), *Shoffner, Sloan, Winters, Canfield and Pilkey* (1953), *Skaller* (1954, 1956), *Crampton* (1955), *Champion* (1955, 1956), *Saeki, Kondo, Himeno, Ikoma, Katsuragi and Tanabe* (1956), *Nordskog, Smith and Phillips* (1959), *Goto and Nordskog* (1959), *Shoffner and Grant* (1960), *Henderson* (1960).

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 $- .436 \pm .132$, 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 ($-.371 \pm .111$). Such regression coefficients are of doubtful value, however, in view of the observation by earlier authors, confirmed by *Bernier, Taylor and Gunns* (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.

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

Table 60

<i>Year of inbreeding</i>	<i>Number of families</i>	<i>Coefficient of inbreeding</i>	<i>Hatchability %</i>
0	10	0	81.04 \pm 2.42
First	6	12.50	69.90 \pm 2.85
	6	25.00	62.50 \pm 3.47
Second	5	25.94	61.70 \pm 7.18
	5	37.50	46.30 \pm 11.59
Third	8	34.37	45.12 \pm 6.33
	5	50.00	43.37 \pm 7.32

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 *Gowe, Johnson, Downs, Gibson, Mountain, Strain and Tinney* (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

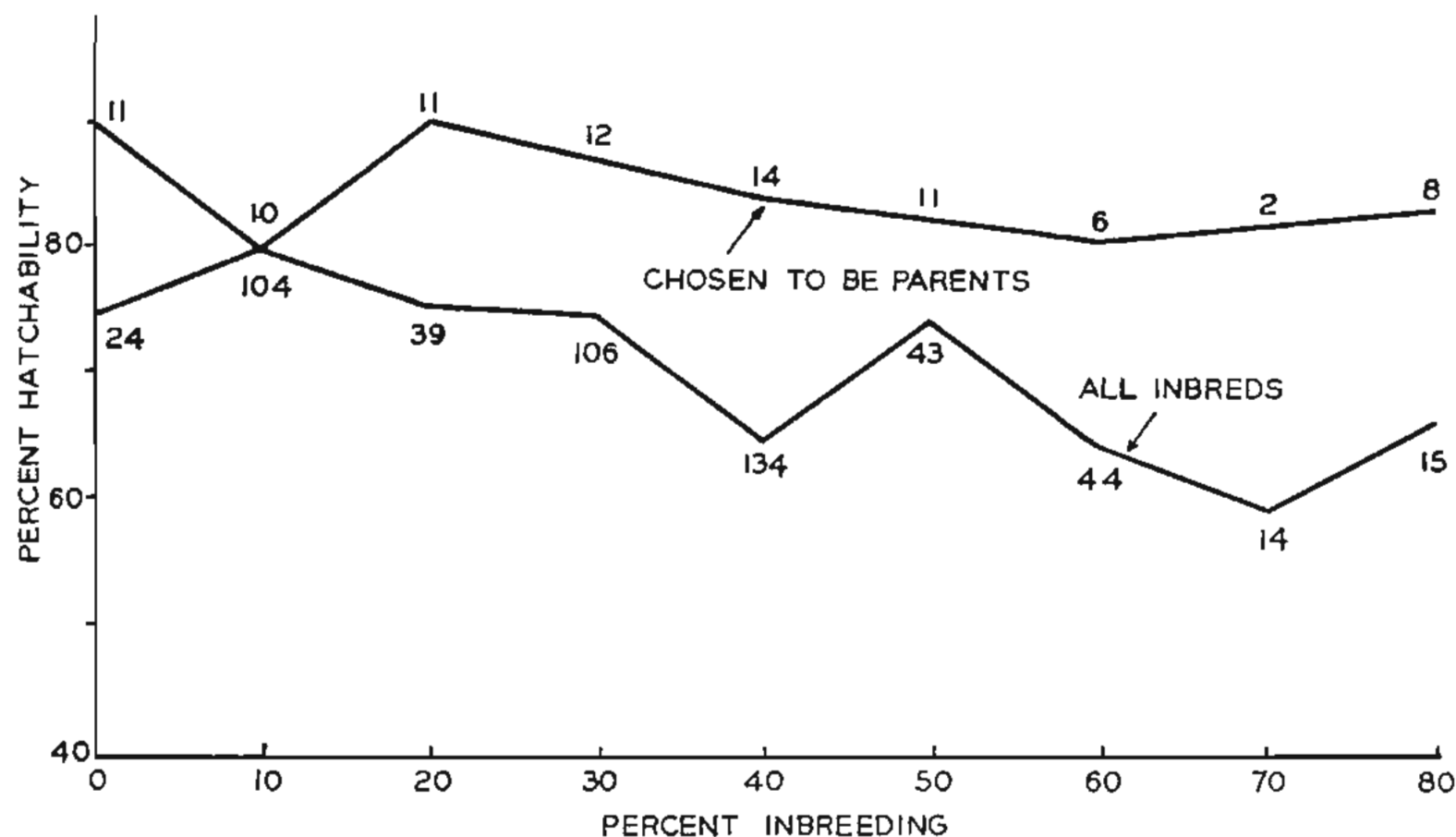


Figure 51

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, 1936 a*).

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 Mitchurinish doctrines, that the unfavorable effects of inbreeding on hatchability can be lessened by factors of the environment in which the animals are raised.

Table 61

Females	Mated to male of same breed		Mated to males of a different breed		Breed (if different) from own)
	Number of fertile eggs	Hatched %	Number of fertile eggs	Hatched %	
White Leghorn					
Strain W	289	61	406	80	Barred Plymouth
" E	167	84	387	86	Rock
" K	132	71	584	80	
White Leghorn	199	73	231	81	Australorp
Australorp	199	72	114	90	White Leghorn

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 $r = 0.21 \pm 0.07$, and 60 White Leghorn dams and their 105 daughters $r = 0.16 \pm 0.09$. 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

<i>Dams' hatchability. Range in %</i>	<i>Number of dams</i>	<i>Mean of dams' hatchability %</i>	<i>Number of daughters</i>	<i>Mean of daughters' hatchability %</i>
68.0—94.5	51	80.63 \pm 0.67	105	75.10 \pm 1.91
41.0—67.5	23	59.95 \pm 1.16	43	66.36 \pm 2.94
Difference		20.68 \pm 1.33		8.74 \pm 3.81

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

Table 63

<i>Dams' hatchability. Range in %</i>	<i>Number of dams</i>	<i>Mean of dams' hatchability %</i>	<i>Number of daughters</i>	<i>Mean of daughters' hatchability %</i>
74.0—94.5	36	81.24 \pm 0.53	62	63.40 \pm 2.85
53.0—73.5	24	64.36 \pm 1.13	43	52.33 \pm 2.88
Difference		16.88 \pm 1.25		11.07 \pm 4.05

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.

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-

Table 64

Coefficient of correlation between	Author	Breed and Number of individuals	Coefficient
Dams and daughters of same males	<i>Hays and Sanborn Bronkhorst</i>	748 Rhode Island Reds	0.059 \pm 0.037
		1061 White Leghorns	0.092 \pm 0.028
Dams and mates of same males	<i>Hays and Sanborn Bronkhorst</i>	647 Rhode Island Reds	0.158 \pm 0.039
		1079 White Leghorns	0.131 \pm 0.030
Mates (average) and daughters (individual) of same males	<i>Hays and Sanborn</i>	412 Rhode Island Reds	0.227 \pm 0.047
First and second-year daughters of same males	<i>Hays and Sanborn</i>	51 Rhode Island Reds	0.300 \pm 0.128
Sires' mates and sons' mates	<i>Hays and Sanborn</i>	170 Rhode Island Reds	0.076 \pm 0.076

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 F_1 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 F_1 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 40.7 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), *Brunson, 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-sire 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 65

<i>Females</i>	<i>Cockerel C 8081</i>		<i>Cockerel E 280</i>	
	<i>Fertility %</i>	<i>Fertile eggs hatched %</i>	<i>Fertility %</i>	<i>Fertile eggs hatched %</i>
C 7129	67	0	97	53
C 7132	100	0	98	55
C 7297	92	0	94	73
C 7310	100	0	89	53
C 7482	88	0	50	0
C 7716	48	10	0	0
C 7738	100	0	100	82

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 1941 b*). 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 Gunns (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. *Baczowska (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 Bögge (1955)*.

Detailed observations by *Bernier* (1947) and *Bernier, Taylor and Gunns* (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 (OB) 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 $+ .103$, 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

Table 66

<i>Correlation between embryo size and hatchability</i>					
<i>Class of eggs</i>	<i>Measurement</i>	<i>Origin of females</i>			
		<i>OB, 1940</i>		<i>SEOB, 1941</i>	
		<i>Number of matings</i>	<i>Correlation</i>	<i>Number of matings</i>	<i>Correlation</i>
All eggs, irrespective of clutch position	Blastoderm size	30	+.137	60	+.125
	Number of somites	29	+.473 ¹	61	+.093
Eggs in first clutch position	Blastoderm size	15	+.291	45	+.128
	Number of somites	13	+.632 ²	47	+.028
Eggs in clutch position subsequent to first	Blastoderm size	30	+.103	57	-.017
	Number of somites	28	+.406 ¹	59	-.044

¹significant at 1% level; ²significant at 5% level

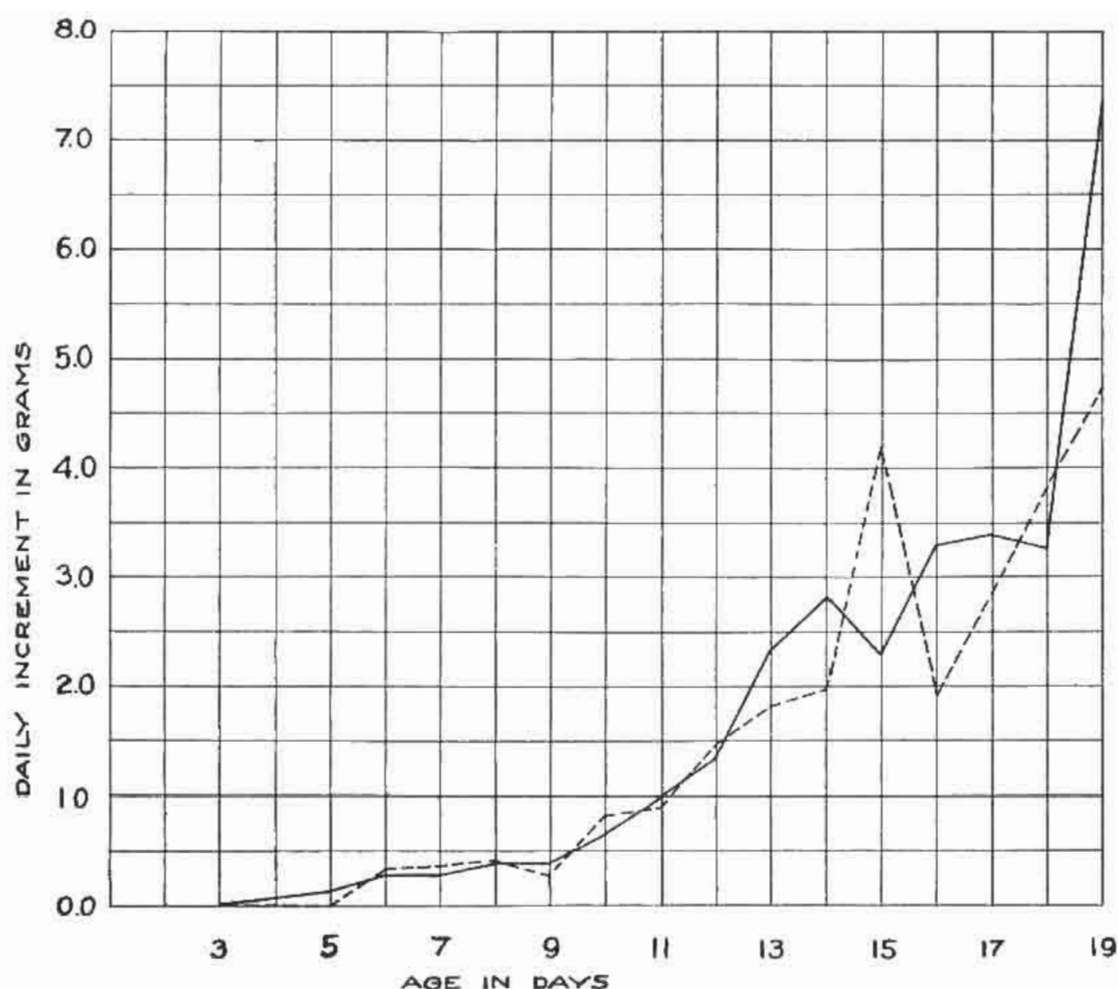


Figure 52

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

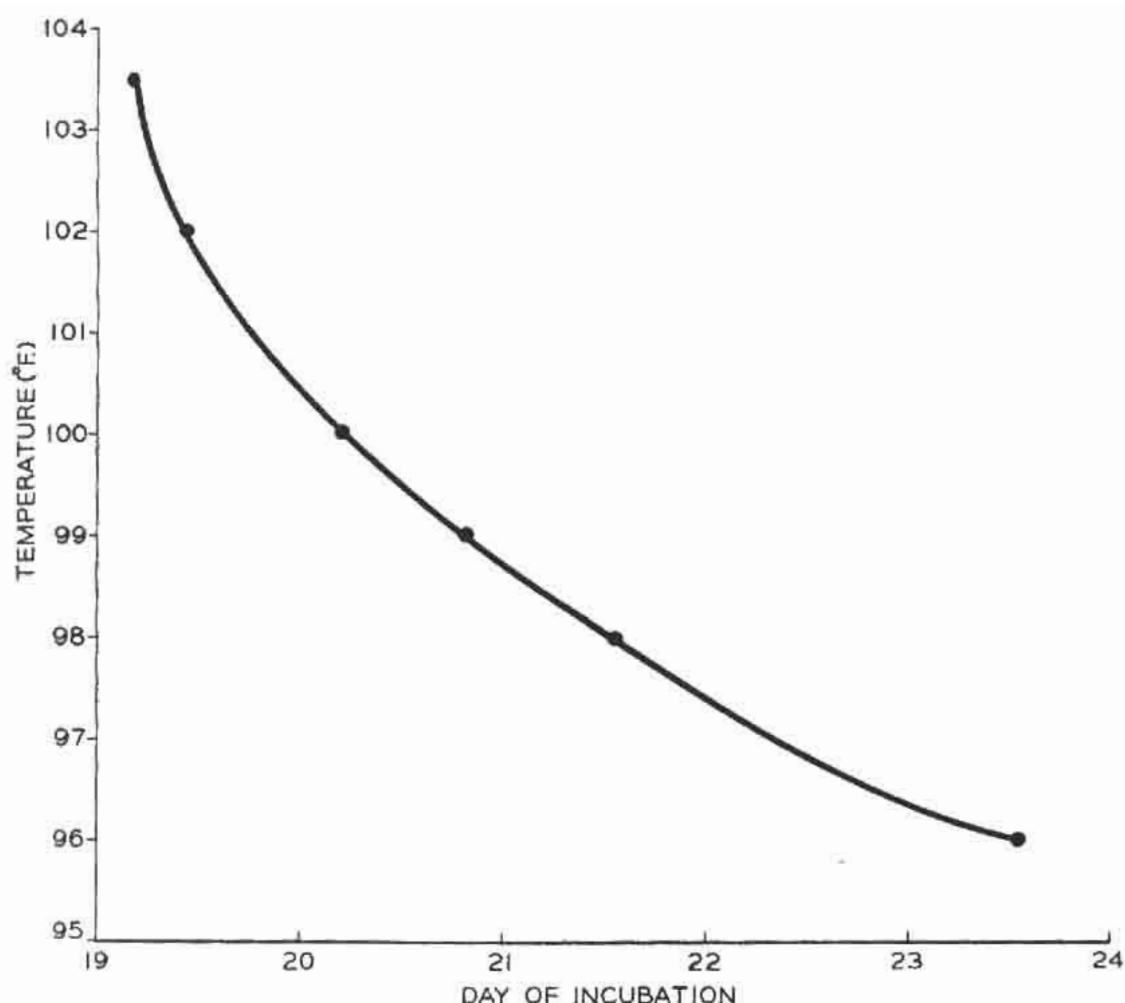


Figure 53

The effect of incubation temperature on time of hatch. (From Barott, 1937).

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 dicephalic 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

<i>Orientation of eggs during incubation</i>		<i>Malpositions</i>			
		<i>I</i>	<i>II</i>	<i>III</i>	<i>IV</i>
Large end up	Average	1.16	1.76	3.38	0.59
	Range	1.08-1.95	0.20-2.12	1.95-3.94	0.03-1.04
Horizontal	Average	1.66	3.67	1.56	3.00
	Range	0.95-1.94	2.27-4.18	1.36-2.14	1.27-4.40

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

<i>Embryo position</i>	<i>Number of eggs</i>	<i>Pipped %</i>
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 (*Polk 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 Storrs 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* (1927 b) 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* (1927 b), *Hutt and Greenwood* (1928-1929 a), *Munro* (1932), *Smith* (1934), and *Otrygan'ev* (1936 c; 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

<i>Mating</i>	<i>Incubation period (1934)</i>	<i>Number of fertile eggs</i>	<i>Number of chondrodys-trophic embryos</i>	<i>Percent of chondrodys-trophic embryos</i>
Frizzle x Frizzle	February 20 to April 3	201	10	4.98
Frizzle x Leghorn	April 10 to April 24	91	3	3.30
Frizzle x Frizzle	May 8 to June 12	209	1	0.50

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, Elvehjem 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. 54) 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, 1957 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).

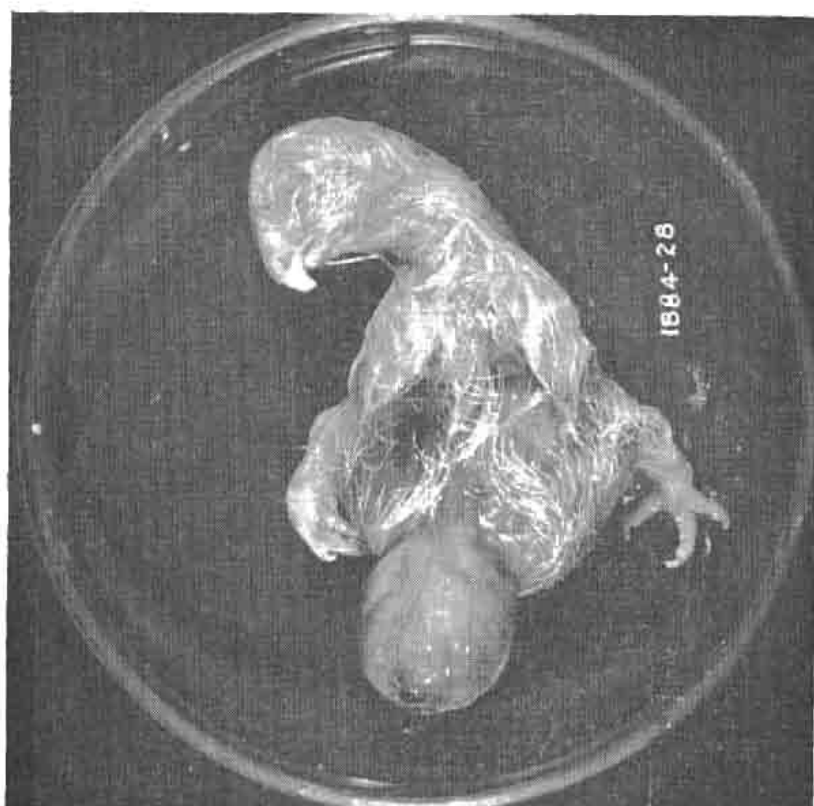


Figure 54

Micromelia and parrot beak as occurring in eggs produced on a biotin deficient diet (From *Cravens, McGibbon and Sebesta, 1944*).

Otrygan'ev and Kuchkovskaia (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 *Ansel* (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

Table 70

<i>Year</i>	<i>Number of fertile eggs</i>	<i>Head abnormalities %</i>
1930	7883	1.29
1931	11121	1.49
1932	9977	0.24
1933	8982	0.19

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 Pintemberger* (1925 a and b, 1927), *Wolff* (1933, 1934, 1936, 1948), *Szepeswöl* (1933, 1934), *Gallera* (1935-1936), *Frölich* (1936), *Morita* (1936, 1937), *Krayevoy* (1938), *Tarnavsky* (1938), *Lallemand* (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 *Lallemand* (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).

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 sils 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

<i>Fertile eggs hatched %</i>	<i>Number of chicks</i>	<i>Chick mortality during the first three weeks %</i>
20 - 39	162	17.90 \pm 1.97
40 - 59	610	12.95 \pm 0.92
60 - 79	595	11.43 \pm 0.88
80 - 99	210	14.76 \pm 1.66

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 Jull (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 Brönkhorst (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,

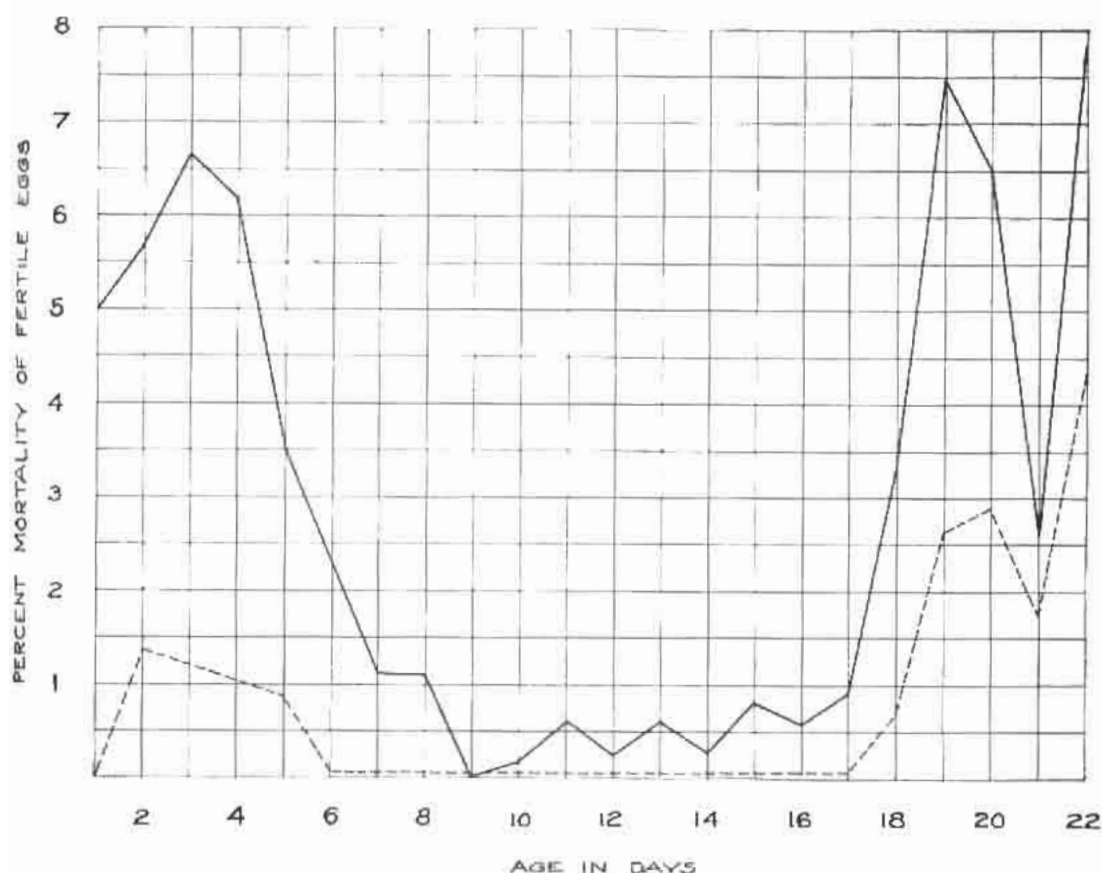


Figure 55

Daily embryonic mortality, in percent of fertile eggs, within a high (---) and a low (—) hatching line of White Leghorns (From Bronkhorst, 1933).

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 F_1 hens (F_2 embryos) than for the first crosses (F_1 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.

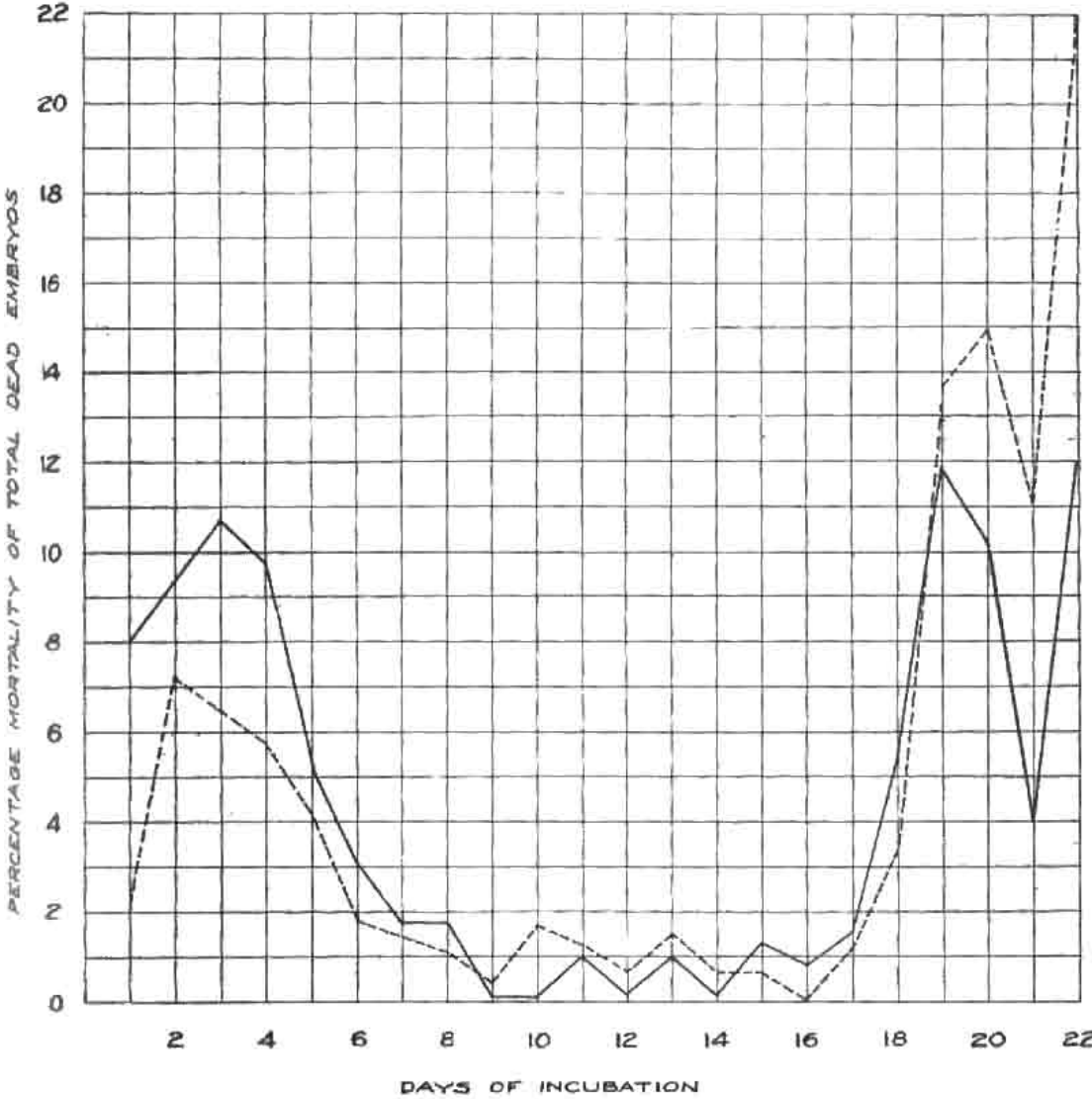


Figure 56

Relative distribution of embryonic mortality within a high (- -) and a low (—) hatching line of White Leghorns (From Brankhorst, 1933).

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 Hesselde, 1939). Observations of Serk (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

Pullorum 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; Dearstyne, Kaupp and Wilfong, 1929; Runnells, 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 Dearstyne, 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

Authors	Non-infected stock			Infected stock		
	Number of laying hens	Number of fertile eggs	Hatch %	Number of laying hens	Number of fertile eggs	Hatch %
Bushnell, Hinshaw and Payne (1926)	164	4583	63.4	19	221	45.2
Beach and Michael (1930)	202	1842	72.2	96	395	56.2

cidence 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 (Runnells and van Roekel, 1926-1927 a and b; Mallmann and Moore, 1936).

Table 73

Mean serum titre	Number of hens	Number of fertile eggs	Hatch %
over 200	9	218	28.4
100 - 200	6	187	36.4
under 100	10	303	45.5

Salmonella aertrycke, 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

Date of test	Titre of serum	Percent hatchability for corresponding period
June 11, 1921	1 : 640	25.3
January 25, 1922	1 : 160	65.7
April 13, 1922	1 : 40	90.6

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

Material	Number tested	Percent positive during entire season	Range of percent positive in different hatches
Unhatched dead chicks	241	51.5	24.3 - 85.1
Newly-hatched chicks	236	11.4	5.0 - 20.4

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 (Buza, 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 (1951 a) 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, Gunns, Grau and Lepkovsky (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 *Schlotthauer 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 (*Bressler and Gordeuk*, 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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LITERATURE AND AUTHOR INDEX¹

- A** (ACHARD), Von Ausbrüten der Eyer durch Elektrizität. Berlinische Sammlungen zur Beförderung der Arzneywissenschaft, der Naturgeschichte, der Haushaltungskunst, Kameralwissenschaft und der dahin einschlagenden Literatur 10, 261-263, 1779. 41
- ABBOTT, U. K., Further studies on diplopodia. II. Embryological features. *Journal of Genetics* 56, 179-196, 1959 a. 156
- ABBOTT, U. K., Further studies on diplopodia. III. The relationship between expressivity and penetrance in selected lines and crosses. *Journal of Genetics* 56, 197-225, 1959 b. 156
- ABBOTT, U. K. and V. S. ASMUNDSON, Scaleless, an inherited ectodermal defect in the domestic fowl. *Journal of Heredity* 48, 63-70, 1957. 132
- ABBOTT, U. K., L. W. TAYLOR and H. ABPLANALP, A second talpid-like mutation in the fowl. (Abstract). *Poultry Science* 38, 1185, 1959. 161
- ACHARD DE PÉATIEUX, De l'incubation artificielle. Bulletin industriel, publié par la Société d'Agriculture, Sciences, Arts et Commerce de l'Arrondissement de St.-Etienne (Loire) 8, 238-244, 1850. 38
- ACKERMANN, W. W. and A. TAYLOR, Application of a metabolic inhibitor to the developing chick embryo. *Proceedings of the Society for Experimental Biology and Medicine* 67, 449-452, 1948. 98
- ADAMS, J. L., W. H. MCGIBBON and L. E. CASIDA, The fertility and hatchability of estrogen-fed pullets and carry-over effects on their progeny. *Poultry Science* 30, 707-712, 1951. 107
- ADAMSTONE, F. B., The effects of vitamin-E deficiency on the development of the chick. *Journal of Morphology and Physiology* 52, 47-80, 1931. 107
- ADRIAN, J., Répercussion des avitaminoses sur le développement embryonnaire chez le mammifère et l'oiseau. *Annales de Zootechnie* 7, 97-122, 1958.
- AGGAZZOTTI, A., Influenza dell'aria rarefatta sull'ontogenesi. I. La perspirazione delle ova di gallina durante lo sviluppo in alta montagna. *Archiv für Entwicklungsmechanik* 36, 633-648, 1913. 61
- AGGAZZOTTI, A., Influence de l'air raréfié sur l'ontogenèse. I. La perspiration des oeufs de poule durant le développement en haute montagne. *Archives Italiennes de Biologie* 59, 287-304, 1913. 61
- ALDROVANDI, U., Ornithologiae tomus alter. Bononiae (Nicolaum Tebaldinum), 1645. 19, 20
- ALLEN, C. J. and L. R. CHAMPION, Competitive fertilization in the fowl. *Poultry Science* 34, 1332-1342, 1955. 130
- ALMQUIST, H. J. and W. F. HOLST, Variability of shell porosity in the hen's egg. *Hilgardia* 6, 61-72, 1931. 85
- ALMQUIST, H. J. and E. MECCHI, Vitamin A requirements of laying hens. *Poultry Science* 18, 129-137, 1939. 93
- ALSOP, F. M., The effect of abnormal temperatures upon the developing nervous system in the chick embryo. *Anatomical Record* 15, 307-324, 1918-1919. 55
- ANCEL, P., Les variations individuelles dans les expériences de tératogenèse. *Revue Scientifique* 83, 99-106, 1945 a. 196
- ANCEL, P., L'achondroplasie. Sa réalisation expérimentale - sa pathogénie. *Annales d'Endocrinologie* 6, 1-24, 1945 b. 194, 196

¹The bibliography may also be used as an author index, a page reference appearing at the end of those publications which have been discussed in the text. Russian names and titles, unless given differently by the authors themselves or taken from abstracting journals, have been transliterated according to the rules of the Library of Congress.

- ANCEL, P., Recherche expérimentale sur le spina bifida. Archives d'Anatomie microscopique et de Morphologie expérimentale 36, 45-68, 1946-1947. 196
- ANCEL, P., Recherche sur la réalisation expérimentale de la célosomie. Archives d'Anatomie, d'Histologie et d'Embryologie 30, 3-21, 1947. 195
- ANCEL, P., La chimiotératogénèse. Paris (G. Doin), 1950. 196
- ANCEL, P., Recherches sur l'action tératogène du refroidissement temporaire de l'oeuf de Poule au cours de l'incubation. Journal of Embryology and Experimental Morphology 6, 335-345, 1958. 56
- ANCEL, P., Recherches sur les malformations déterminées par le refroidissement temporaire de l'oeuf de poule et compatibles avec la vie des Poussins. Journal of Embryology and Experimental Morphology 7, 330-334, 1959. 56
- ANCEL, P., Recherches sur les relations entre l'effet létal et l'effet tératogène de la carence en oxygène chez l'embryon de poule. Acta Anatomica 38, 147-159, 1959.
- ANCEL, P. and S. CALAME, Sur les effets létal et tératogène obtenus à l'aide d'une nouvelle technique du refroidissement temporaire d'oeufs de Poule. Comptes rendus des séances de l'Académie des Sciences 249, 1434-1435, 1959. 56
- ANCEL, P. et P. VINTEMBERGER, Comparaison entre les effets des rayons X et ceux du vieillissement sur l'oeuf de poule. Comptes Rendus Hebdomadaires des Séances de la Société de Biologie 92, 1401-1403, 1925 a. 53, 196
- ANCEL, P. et P. VINTEMBERGER, Étude de l'action des rayons X sur le développement embryonnaire. Les rayons X ont-ils une action accélératrice? Archive de Biologie 35, 1-43, 1925 b. 196
- ANCEL, P. et P. VINTEMBERGER, Influence de la température sur la radiosensibilité d'oeufs d'oiseaux et de batraciens. Comptes Rendus Hebdomadaires des Séances de la Société de Biologie 97, 796-799, 1927. 196
- ANCEL, S., Action de divers gaz sur l'oeuf de poule. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 186, 1579-1580, 1928. 53, 67
- ANCEL, S., Recherches sur la toxicité cellulaire de poisons gazeux et volatils. Étude faite sur l'oeuf de Poule. Archives d'Anatomie, d'Histologie et d'Embryologie 8, 433-481, 1928; 9, 3-169, 1928-1929. 53
- ANDRÄ, E., Zusammenhänge zwischen Legeleistung, Befruchtung, Schlupf und Aufzucht beim Huhn. Archiv für Geflügelkunde 12, 284-305, 1938.
- ANGELL, J. M., Practical methods of cabinet incubation. Official Report. Eighth World's Poultry Congress Copenhagen 1948, 1, 326-331, 1948.
- ANGHI, G. G., Adatok a tyuktojás ehető részeinek színének és héjsúlyának viszonyosságáról. (Data on the relationship between the edible parts, the color and the weight of the shell of hen's eggs). Kísérletügyi közlemények 43, 55-67, 1941. 74
- ANONYMOUS, Hünen über einer brennenden Lampe auszubrüten. Sammlung kleiner Ausführungen aus verschiedenen Wissenschaften, welche in dem hiezu gewidmeten Theile der von Johannis 1750, bis zum Ende des 1751 ten Jahrs wöchentlich ausgegebenen Hannoverschen Anzeigen stückweise bekannt gemacht sind 1, 654, 1752.
- ANONYMOUS, (On artificial incubation). Nützlicher und getreuer Unterricht für den Land- und Bauersmann auf das Jahr 1772 oder fortgesetzter allgemeiner Landwirtschafts-Kalender 3, 42-48, 1772.
- ANONYMOUS, (On artificial incubation). Nützlicher und getreuer Unterricht für den Land- und Bauersmann auf das Jahr 1773 oder fortgesetzter allgemeiner Landwirtschafts-Kalender 4, 16-18, 1773.
- ANONYMOUS, (On artificial incubation). Nützlicher und getreuer Unterricht für den Land- und Bauersmann auf das Jahr 1774 oder fortgesetzter allgemeiner Landwirtschafts-Kalender 5, 32-34, 1774.

- ANONYMOUS, Anweisung wie man junge Hühner in Pferdedünger ausbrüthen kann. Der Patriotischen Gesellschaft in Schlesien neue Oekonomische Nachrichten auf das Jahr 1781, pp. 109-110. Breslau. 39
- ANTINORI, V., Notizie istoriche relative all' Accademia del Cimento. In: Saggi di naturali esperienze fatte nell' Accademia del Cimento. Terza edizione fiorentina. Firenze (Tipografia Galileiana), 1841. 22
- ARBUCKLE, H. B., Report of an investigation as to cause of death of chicks in shell in artificial incubation. *Journal of the Elisha Mitchell Scientific Society* 34, 141-145, 1918-1919.
- ARISTOTLE, The Works of Aristotle, vol. 4, *Historia Animalium*, p. 559. Oxford (Clarendon Press), 1910. 17, 20, 23
- ARSCOTT, G. H. and G. F. COMBS, Further evidence for an unidentified hatchability factor in condensed fish solubles. *Poultry Science* 32, 730-733, 1953.
- ARSCOTT, G. H., M. S. SHORB and U. BOGGS, Effect of vitamin B₁₂ and anti-metabolites of vitamin B₁₂ on chick hatchability. *Poultry Science* 34, 986-988, 1955. 100
- ARSCOTT, G. H., G. B. SWEET and G. F. COMBS, Effect of iodinated casein in a simplified diet on hatchability of chicken eggs. *Poultry Science* 33, 1283-1286, 1954.
- ASHBY, E., Notes on the mound-building birds of Australia, with particulars of features peculiar to the Mallee-Fowl, *Leipoa ocellata*, Gould, and a suggestion as to their origin. *Ibis* 11th series 4, 702-709, 1922. 5
- ASHBY, E., Notes on the unique methods of nidification of the Australian Mallee-Fowl (*Leipoa ocellata*) with original data supplied by Bruce W. Leake. R.A.O.U. *Auk N.S.* 46, 294-305, 1929. 5
- ASKAR, M., Egyptian methods of incubation. Report of Proceedings of the World's Poultry Congress, Ottawa, Canada, July 27 to August 4, 1927, pp. 151-156. 19
- ASMUNDSON, V. S., Abnormal upper mandible. A new lethal mutation in the domestic fowl. *Journal of Heredity* 27, 401-404, 1936. 142-144
- ASMUNDSON, V. S., The position of turkey, chicken, pheasant, and partridge embryos that failed to hatch. *Poultry Science* 17, 478-489, 1938. 191-193
- ASMUNDSON, V. S., Some factors affecting hatchability of eggs. *Poultry Science* 18, 399, 1939. 150
- ASMUNDSON, V. S., Note on the sex ratio and mortality in turkeys. *American Naturalist* 75, 389-393, 1941. 170, 171
- ASMUNDSON, V. S., An inherited micromelia in the domestic fowl. *Journal of Heredity* 33, 328-330, 1942. 150
- ASMUNDSON, V. S., Crooked neck dwarf in the domestic fowl. *Journal of Heredity* 36, 173-176, 1945. 153, 154
- ASMUNDSON, V. S. and F. W. LORENZ, Hybrids of ring-necked pheasants, turkeys and domestic fowl. *Poultry Science* 36, 1323-1334, 1957. 167
- (ASTRUC, J.), Mémoires pour l'histoire naturelle de la province de Languedoc. Paris (G. Cavelier), 1737. 43
- ATKINSON, L. B., The scientific principles of artificial incubation. *Journal of the Royal Society of Arts* 73, 37-55, 62-82, 1925.
- ATWOOD, H., Some factors affecting the weight, composition and hatchability of hen eggs. West Virginia University, Agricultural Experiment Station Bulletin 115, 1914.
- ATWOOD, H., The production of eggs for hatching. West Virginia Agricultural Experiment Station Circular 24, 1916.
- ATWOOD, H., The incubation of hen eggs. West Virginia Agricultural Experiment Station Circular 25, 1917.

- ATWOOD, H., The weight of eggs in connection with the time of the day when they are laid. *Poultry Science* 6, 108-109, 1926-1927. 123
- ATWOOD, H. A balanced and an unbalanced ration fed prior to the hatching season as affecting the hatchability of eggs and the vigor of the progeny. West Virginia University, Agricultural Experiment Station Bulletin 207, 1927.
- ATWOOD, H., and C. E. WEAKLEY, JR., Amount of carbon dioxide given off by eggs during incubation. West Virginia Agricultural Experiment Station Bulletin 185, 1924.
- AXELSSON, J., Variation and heredity of some characters in White Leghorns, Rhode Island Reds and Barnevelders. Part I. *Lunds Universitets Arsskrift N.F., Afd. 2*, 28, No. 4, pp. 1-196, 1932 a. 69, 70, 77-84, 114
- AXELSSON, J., Vissa fodermedels inflytande på äggskallets porositet och därmed på hönsäggens kläckbarhet. *Nordisk Jordbruksforskning* pp. 129-140, 1932 b. 88
- AXELSSON, J., Influence of some factors on hatchability of chicken eggs and on growth rates of embryos and chicks. *Kungl. Lantbrukshögskolans Annaler* 21, 81-103, 1954. 68, 79
- AZALUS, P., Liber Pompilii Azali Placentini: de omnibus rebus naturalibus quae continentur in munde videlicet. Coelestibus et terrestribus necnon mathematicis. Et de angelis motoribus quae coelorum. Venetiis (Apud O. Scotum). 1544 (Author: Giovanni de Fontana. Written in 15th century. In title "motoribus quae" misprint for "motoribusque"). 17, 26
- BAĆZKOWSKA, H., Przyczyny i znaczenie różnic w wielkości zarodków kur i kaczek w pierwszych dwóch dobach wylęgania (Causes and significance of size differences in fowl and duck embryos in the first two days of incubation). *Rocznik Nauk Rolniczych B* 74, 179-197, 1959. 184
- von BAER, K. E., Nachrichten über Leben und Schriften des Herrn Geheimraths Dr. Karl Ernst von Baer, mitgetheilt von ihm selbst. St. Petersburg (H. Schmitzdorff), 1866. 44
- BAINTNER, K. and J. BÖGRE, A csirakorong vizsgálat jelentősége és gyakorlati alkalmazása (The importance of the germinal disc examination and its practical application). *Baromfiipar* 1955, July/August, pp. 10-17. Quoted from *Animal Breeding Abstracts* 24, 295, 1956. 184, 186
- BAKER, R. C., F. W. HILL, A. van TIENHOVEN and J. H. BRUCKNER, The effect of Nicarbazin on egg production and egg quality. *Poultry Science* 36, 718-726, 1957. 136
- BALLOUN, S. L., Choline and tallow in breeder hen diets. *Poultry Science* 35, 737-738, 1956. 110
- BALLOUN, S. L. and R. E. PHILLIPS, Interaction effects of vitamin B₁₂ and pantothenic acid in breeder hen diets on hatchability, chick growth and livability. *Poultry Science* 36, 929-934, 1957. 98
- BANNER, E. L., The history and development of artificial incubation. M. S. Thesis, Cornell University, Ithaca, N.Y., 1916. 46
- BARANCHEEV, L. M., The evaluation of an incubated egg by the intensity of the yolk colouring. (In Russian). *Problems of Animal Husbandry (Moscow)* 1936, No. 7, 147-148. 91
- BARANOVSKAJA, T. I., Zavisimostj inkubacionnyh kačestv jaic ot vozrasta kur i petuhov (The relation between the incubating character of eggs and the age of hens and cocks). *Izv. Timirjazev Sel.-hoz. Akad.* 1957, pp. 161-164. Quoted from *Animal Breeding Abstracts* 25, 427, 1957. 116
- BARBAS, W. C., Over den invloed van het vruchtbaarheids-vitamin op eierleggende kippen. *Landbouwkundig Tijdschrift* 48, 669-678, 1936. 107
- BARFURTH, D., Versuche über die parthenogenetische Furchung des Hühnereies. *Archiv für Entwicklungsmechanik* 2, 303-351, 1895. 128

- BARLOW, J. H., *The Art and Method of Hatching and Rearing All Kinds of Domestic Poultry and Game Birds by Steam*, London, 1824. 43
- BARNETT, B. D., D. J. RICHIEY and C. L. MORGAN, Effect of beta-aminopropionitrile on reproduction of chickens. *Proceedings of the Society for Experimental Biology and Medicine* 95, 101-104, 1957. 109
- BARNUM, G. L., The vitamin E content of eggs as related to the diet of the hen and to hatchability. *Journal of Nutrition* 9, 621-635, 1935. 107
- BAROTT, H. G., Effect of temperature, humidity, and other factors on hatch of hens' eggs and on energy metabolism of chick embryos. U.S. Department of Agriculture Technical Bulletin 553, 1937. 58-60, 65, 66, 188, 189
- BARRETT, C. and L. S. CRANDALL, Avian mound builders and their mounds. *Bulletin New York Zoological Society* 34, 106-127, 1931. 5
- BARTHOLIN, T., *Thomae Bartholini Historiarum Anatomicarum Rariorum Centuria III & IV*. Hafniae (Typis Petri Hakii), 1657. 24
- BARTHOLIN, T., *Thomae Bartholini Historiarum Anatomicarum & Medicarum Rariorum Centuria V & VI. Accessit Viri Clarissimi Joannis Rhodii Mantissa Anatomica*. Hafniae (Typis Henrici Gødiani), 1661. 22, 23
- BARTSCH, O., Temperaturen im Brutei. *Archiv für Kleintierzucht* 3, 221-235, 1943.
- BAUDRIMONT, A. et MARTIN SAINT-ANGE, Recherches sur les phénomènes physiologiques de l'incubation. *Comptes Rendus des Séances de l'Académie des Sciences* 17, 1343-1346, 1843. 55, 58, 65
- BAUDRIMONT, A. et MARTIN-SAINT-ANGÉ, Recherches sur les phénomènes chimiques de l'évolution embryonnaire des oiseaux et des batraciens. *Annales de Chimie et de Physique* 3 ème série 21, 195-295, 1847. 55, 58, 65
- BAUDRIMONT, A. et G. J. MARTIN SAINT-ANGE, Recherches anatomiques et physiologiques sur le développement du fœtus, et en particulier sur l'évolution embryonnaire des oiseaux et des batraciens. *Mémoires présentés par divers savants à l'Académie des Sciences de l'Institut de France* 11, 469-692, 1851. 65
- BAUERNFEIND, J. C. and L. C. NORRIS, The antidermatosis vitamin required for reproduction in the domestic fowl. *Science* 89, 416-417, 1939 a. 97
- BAUERNFEIND, J. C. and L. C. NORRIS, The role of the antidermatosis vitamin and a new water-soluble growth factor in the nutrition of the mature fowl. *Journal of Nutrition* 18, 579-591, 1939 b. 97
- BAUERNFEIND, J. C., A. E. SCHUMACHER, A. Z. HODSON, L. C. NORRIS and G. F. HEUSER, A new factor for growth and reproduction in the domestic fowl. *Proceedings of the Society for Experimental Biology and Medicine* 39, 108-111, 1938.
- BEACH, J. R. and S. T. MICHAEL, Pullorum disease (Bacillary white diarrhea of chickens). *California Agricultural Experiment Station Bulletin* 486, 1930. 200
- BEAN, K. C. and D. W. MacLAURY, The bacterial contamination of hatching eggs and methods for its control. *Poultry Science* 38, 693-698, 1959. 48
- BEARSE, G. E. and M. W. MILLER, The effect of varying levels of vitamin A in the hen ration on the vitamin A content of the egg yolk, on hatchability and on chick livability. *Poultry Science* 16, 39-43, 1937. 93
- BEAUDETTE, F. R., L. D. BUSHNELL and L. F. PAYNE, Study of an organism resembling *Bact. pullorum* from unabsorbed yolk of chicks "dead in shell." *Journal of Infectious Diseases* 32, 124-132, 1923. 200
- BECHER, H., Über die Embryonalentwicklung bei verschiedenen atmosphärischen Druckverhältnissen. *Anatomischer Anzeiger* 88, Ergänzungsheft, 144-154, 1939. 64
- BECKER, W. A. and G. E. BEARSE, Pre-incubation warming and hatchability of chicken eggs. *Poultry Science* 37, 944-948, 1958. 50

- BECKWITH, T. D. and G. T. HORTON. Is the poor hatching of normal eggs due to the presence of microorganisms within the eggs? *Science N.S.* 40, 240, 1914. 201
- BEGUELIN, Méthode de faire éclore des poulets au moyen d'un feu de Lampe. *Bibliothèque Impartiale, pour les mois de Juillet et Août 1750*, 2, première partie, Leiden, 1750, pp. 105-124. 38
- BEGUELIN, Mémoire sur l'art de couvrir les oeufs ouverts. *Histoire de l'Académie Royale des Sciences et Belles Lettres à Berlin* 5, (année 1749), 71-83, 1751. Reprinted in: *Collection Académique, Partie Etrangère* 8, 162-171, 1770. 37
- BEGUELIN, Herrn Beguelins Abhandlung von der Kunst, geöffnete Eyer beym Lampenfeuer auszubrüten. Aus dem Französischen übersetzt und mit Anmerkungen erläutert von D. Joh. Georg Krünitz. *Hamburgisches Magazin oder gesammelte Schriften, aus der Naturforschung und den angenehmen Wissenschaften überhaupt* 19, 118-156, 1757. (German translation of preceding two articles). 38
- BELON, P., Les Observations de plvsievs singlaritez et choses memorables, trouuées en Grece, Asie, Iudée, Egypte, Arabie, & autres pays estranges, redigées en trois liures. Paris (Guillaume Cauellat), 1553. 19
- BENEDICT, F. G., W. LANDAUER and E. L. FOX, The physiology of normal and Frizzle fowl, with special reference to the basal metabolism. *Storrs Agricultural Experiment Station Bulletin* 177, 1932. 131
- BENJAMIN, E. W., A study of selections for the size, shape and color of hens' eggs. *Cornell University Agricultural Experiment Station Memoir* 31, 1920. 67, 74
- BENTLEY, O. G. and T. V. HERSHBERGER, The effect of antibiotics on hatchability of hens' eggs and progeny growth performance. *Poultry Science* 33, 641-648, 1954. 101
- BERG, L. R. and G. E. BEARSE, The effect of water-soluble vitamins and energy level of the diet on the performance of laying pullets. *Poultry Science* 35, 945-951, 1955.
- BERG, L. R., G. E. BEARSE, J. MCGINNIS and C. F. McCLARY, Vitamin B₁₂ in the nutrition of the laying hen. *Poultry Science* 31, 488-496, 1952. 100
- BERGTOLD, W. H., A Study of the Incubation Periods of Birds. Denver (Kendrick-Bellamy Co.), 1917.
- BERNAL, J. D., The Social Function of Science. London (George Routledge & Sons), 1939. 46
- BERNARD, C., Diverses anomalies d'oeufs de poule. *Comptes rendus des Séances et Memoirs de la Société de Biologie* 1, 9-10, 1850. 74
- BERNIER, P. E., The relative effects of inbreeding and outbreeding on reproduction in the domestic fowl. Ph.D. Thesis, University of California, 1947. 119, 120, 125, 126, 175, 185, 186
- BERNIER, P. E., Micromelia VII, an overdominant recessive lethal in the domestic fowl. *Records of the Genetics Society of America* 20, 89, 1951. 156
- BERNIER, P. E., A dominant lethal in S. C. White Leghorns (Abstract). *Poultry Science* 32, 889-890, 1953. 166
- BERNIER, P. E., A spontaneous chromosome aberration in a S. C. White Leghorn. (Abstract). *Poultry Science* 39, 1234, 1960. 166
- BERNIER, P. E. and T. COONEY, Black down colour and riboflavin deficiency in embryos of the domestic fowl. Report of Proceedings, Tenth World's Poultry Congress, Edinburgh, Scotland 13th-21st August, 1954. Part II, Section papers, pp. 66-71, 1954. 163, 164, 166
- BERNIER, P. E., L. W. TAYLOR and C. A. GUNNS, The relative effects of inbreeding and outbreeding on reproduction in the domestic fowl. *Hilgardia* 20, 529-628, 1951. 119, 120, 123, 125, 126, 128, 131, 175, 185

- BETHKE, R. M., D. C. KENNARD and V. D. CHAMBERLIN, The relation of nutrition to production and hatchability of chicken eggs. II. Effects of choline chloride, methionine, and certain animal and marine products. *Poultry Science* 25, 579-583, 1946.
- BETHKE, R. M., D. C. KENNARD and V. D. CHAMBERLIN, The relation of nutrition to production and hatchability of chicken eggs. III. Effect of pantothenic acid, nicotinic acid, pyridoxine, folic acid, biotin, and certain marine products. *Poultry Science* 26, 377-380, 1947.
- BETHKE, R. M., P. R. RECORD and D. C. KENNARD, Relation of the vitamin G complex to hatchability and nutritive value of eggs. Abstract. *Poultry Science* 12, 332-333, 1933. 94
- BETHKE, R. M., P. R. RECORD and D. C. KENNARD, The relation of vitamin G to the hatchability of hens' eggs. *Journal of Nutrition* 12, 297-307, 1936. 94
- BETHKE, R. M., P. R. RECORD, D. C. KENNARD and V. D. CHAMBERLIN, The relation of nutrition to production and hatchability of chicken eggs. I. Effect of protein supplements and alfalfa meal. *Poultry Science* 25, 570-578, 1946. 109
- BETHKE, R. M., P. R. RECORD and F. W. WILDER, The effect of the ration of the hen on the vitamin G content of eggs with observations on the distribution of vitamins B and G in normal eggs. *Journal of Nutrition* 12, 309-320, 1936. 94
- BICE, C. M. and B. A. TOWER, Crossbreeding poultry for meat production including a feeding test of taro waste and poi. Hawaii Agricultural Experiment Station Bulletin 81, 1933. 175
- du BIGNON, B., Extrait d'une lettre de M. Baussau du Bignon à M. de Réaumur contenant quelques expériences pour faire éclore des poulets par la fermentation du tan. *Mémoires de Mathématique et de Physique présentés à l'Académie Royale des Sciences* 4, 483-489, 1763. 40
- BIRCH, T., The history of the Royal society of London for improvement of natural knowledge, from its first rise. London (A. Miller), 1756-1757. 29, 31, 32
- BIRD, H. R. and J. A. MARVEL, Relation of diet to hatchability of eggs produced in batteries and in open-front houses. *Poultry Science* (Abstract 21, 465, 1942) 22, 403-410, 1943.
- BIRD, H. R., M. RUBIN and A. C. GROSCHKE, An inborn characteristic determining the response of chickens to a diet free of animal protein. *Journal of Nutrition* 33, 319-330, 1947. 110
- BIRD, H. R., M. RUBIN and A. C. GROSCHKE, Relation of an unidentified dietary factor to the utilization of vegetable proteins by chickens. Official Report. Eighth World's Poultry Congress Copenhagen 1948, 1, 187-194, 1948.
- BIRD, H. R., M. RUBIN, D. WHITSON and S. K. HAYNES, Effectiveness of dietary supplements in increasing hatchability of eggs and viability of progeny of hens fed a diet containing a high level of soybean oil meal. *Poultry Science* 25, 285-293, 1946. 109, 110
- BIRD, S., Fecundity and reproductive ability in closely confined fowl. *Scientific Agriculture* 17, 359-375, 1937.
- BISBEY, B., V. APPLEBY, A. WEIS and S. COVER, The vitamins A and D activity of egg yolks of different color concentrations. Missouri Agricultural Experiment Station, Research Bulletin 205, 1934. 91
- BISWAL, G. and C. C. MORRILL, The pathology of the reproductive tract of laying pullets affected with Newcastle disease. *Poultry Science* 33, 880-897, 1954. 202
- BLACK, D. J. G., J. GETTY, M. E. COATES, G. F. HARRISON and S. K. KON, Hatchability of eggs and the production of chicks for the assay of vitamin B₁₂. *Biochemical Journal* 46, VIII, 1950. 100
- BLACK, D. J. G., R. C. JENNINGS, T. R. MORRIS and J. A. PALGRAVE, A depressant effect of a white fish meal on hatchability. Report of Proceedings, Tenth World's Poultry Congress, Edinburgh, Scotland 13th-21st August, 1954. Part II. Section papers, pp. 121-125, 1954.

- BLACK, D. J. G., T. R. MORRIS and J. A. PALGRAVE. The value of a grass sward for breeding hens. *Poultry Science* 36, 780-788, 1957.
- BLAMBERG, D. L., U. B. BLACKWOOD, W. C. SUPPLEE and G. F. COMBS. Effect of zinc deficiency in hens on hatchability and embryonic development. *Proceedings of the Society for Experimental Biology and Medicine* 104, 217-220, 1960. 111
- BLAMPIGNON, F. A., *Étude sur Malebranche*. Paris (C. Douniol), 1861. 36
- BLATTNER, R. J. and A. P. WILLIAMSON. Developmental abnormalities in the chick embryo following infection with Newcastle disease virus. *Proceedings of the Society for Experimental Biology and Medicine* 77, 619-621, 1951. 202
- BLESS, A. A. and A. L. ROMANOFF. Stimulation of the avian embryo by x-rays. *Journal of Cellular and Comparative Physiology* 21, 117-121, 1943. 56
- BLOW, W. L. and E. W. GLAZENER. The effect of inbreeding on some production characters in poultry. *Poultry Science* 32, 696-701, 1953. 175
- BLYTH, J. S. S. Infertility and embryonic mortality in the domestic fowl. *Proceedings of the Royal Society of Edinburgh B* 62, Part II, 191-201, 1945. 128
- BOCK, H., *Kreutterbuch*. Strassburg (J. Rihel), 1577 (first edition 1539). 19
- BÖGRE, J. and I. VARGA. A csirakorong vizsgálata újabb eredményei (New results of the germinal disc examination). *Baromfiipar* 1956, pp. 190-194. 186
- BOELUM, J., Vitamin A requirements of laying pullets. Official Report. Eighth World's Poultry Congress Copenhagen 1948, 1, 81-85, 1948. 93
- BOLTON, W., The effect of the age of the hen on the porosity of the egg. *Journal of Agricultural Science* 49, 383-386, 1957. 82
- BONNEMAIN, Observations sur l'art de faire éclore et d'élever la volaille sans le secours des poules, ou Examen des causes qui ont pu empêcher de donner suite aux diverses tentatives qui ont été faites en Europe, pour imiter les Égyptiens dans l'art de faire éclore et d'élever les oiseaux domestiques de toutes espèces, par le moyen d'une chaleur artificielle; suivi des procédés qu'il faudrait employer pour amener cet art à sa perfection. Paris, 1816. 41, 44
- BONNEMAIN, Description d'un appareil destiné à chauffer l'eau ou tout autre liquide et à la maintenir constamment au même degré de chaleur. *Bulletin de la Société d'encouragement pour l'industrie nationale* 23, 238-242, 1824. 41, 42, 44
- BONNEMAIN, On artificial incubation, or hatching poultry in stoves heated by hot water continually circulating through them, the fire being also regulated by a pyrometer; and which methods are also peculiarly applicable to heating hot-houses, green-houses, etc. *Gill's Technological Repository; or, Discoveries and Improvements in the Useful Arts* 2, 65-73, 1828. 41, 42, 44
- BONNFS, M., Essai sur l'incubation artificielle, ou l'art de faire éclore les poulets et toute espèce d'oiseaux dans certains appareils, par le moyen du calorique. Toulouse (B. Cadet), 1831. 43
- BORISSENKO, E. I., The changes of internal conditions of development under the influence of inbreeding. (Russian with English summary). *Moskovskaia ordena Lenina Sel'skokhozia ietvennaia Akademiia imeni K. A. Timiriazeva Trudy* No. 27, 1945. 175
- BORNE, Notice sur la formation d'un établissement-modèle ayant pour objet l'incubation artificielle et la première éducation des poulets, sous la direction du sieur Borne. Paris (Imprimerie Decourchant), 1828. 43, 44
- BOSE, Extrait d'un rapport fait à la Classe des sciences physiques et mathématiques de l'Institut par M. Bose, au nom d'une Commission, chargée d'examiner une méthode proposée par Mademoiselle Portebois, pour faire couvrir à volonté les volailles mâles et femelles pendant toute l'année. *Bulletin de la Société d'encouragement pour l'industrie nationale* 12, 168-170, 1813. 42

- BOUCHER, R. V., E. G. BUSS and A. J. G. MAW, Physiological characteristics associated with a mutant gene in chickens that causes a deficiency of riboflavin. 2. Blood. (Abstract). *Poultry Science* 38, 1190, 1959. 97
- BOUGES, L. C., Recherches sur les conditions optima de l'incubation artificielle des oeufs de poules. Thèses présentées à la Faculté des Sciences de Toulouse, No. d'ordre 27, 1923. 53, 79, 188
- la BOULLAYE, Les Voyages et Observations du Sievr de la Bovllaye-Le-Govz Gentil-Homme Angevin, où sont décrites les Religions, Gouuernemens, & situations des Estats & Royaumes d'Italie, Grece, Natolie, Syrie, Perse, Palestine, Katamenie, Kaldée, Assyrie, Grand Mogol, Bijapour, Indes Orientales des Portugais, Arabie, Egypte, Hollande, grande Bretagne, Irlande, Dannemark, Pologne, Isles & autres lieux d'Europe, Asie & Affrique, ou il a seiourné, le tout enrichy de belles figures. Paris (Gervais Clovisier), 1657, (First edition 1653). 19
- BOYD, J. L., Forty-first Annual Report of the Agricultural Experiment Station of the Michigan State College for the year ending June 30, 1928, pp. 183-184. 105
- BRADLEY, R., The Country Gentleman and Farmer's Monthly Director. 6th edition. London (D. Browne), 1736. 40
- BRANION, H. D., Minerals in poultry nutrition. *Scientific Agriculture* 18, 217-276, 1938.
- BRANION, H. D. and J. B. SMITH, The influence of vitamin D on hatchability and egg production. *Poultry Science* 11, 261-265, 1932. 105
- BRECHEMIN, L., La Basse-Cour Productive. 8^{ème} edition. Paris (Librairie Agricole de la Maison Rustique), 1926. 41
- BRESSLER, G. O. and S. GORDEUK, Jr., Effect of cecal coccidiosis on body weight, egg production and hatchability in chickens. *Poultry Science* 30, 509-511, 1951. 203
- BRIGGS, G. M., A. C. GROSCHE and R. J. LILLIE, Effect of proteins low in tryptophane on growth of chickens and on laying hens receiving nicotinic acid-low rations. *Journal of Nutrition* 32, 659-675, 1946. 98
- BRIGHAM, A. A., Carbon-dioxide in incubators. Fourteenth Annual Report of the Rhode Island Agricultural Experiment Station 1900-1901, 300-303, 1901. 65
- BRILES, W. E., Evidence for overdominance of the B blood group alleles in the chicken (Abstract). *Records of the Genetics Society of America* 23, 34-35, 1954. 176
- BRILES, W. E. and W. F. KRUEGER, The effect of parental B blood group genotypes on hatchability and livability in Leghorn inbred lines (Abstract). *Poultry Science* 34, 1182, 1955. 176, 197
- BRILL, G. D., Chinese incubators. Seventeenth Annual Report of the Bureau of Animal Industry, U.S. Department of Agriculture, for the year 1900, pp. 247-253, 1901.
- BROADFOOT, D. I. and W. M. SMITH, Jr., Effects of infectious bronchitis in laying hens on egg production, percent unsettable eggs and hatchability. *Poultry Science* 33, 653-654, 1954. 202
- BROCA, P., Expériences sur les oeufs à deux jaunes. *Annales des Sciences Naturelles* 4^{ème} série, *Zoologie* 17, 78-87, 1862. 74
- BROCKHUIZEN, E. G. and M. van ALBADA, A hereditary lethal abnormality of the beak in Barnevelders. *Genetica* 26, 415-429, 1953. 156-158
- BROCKHUIZEN, E. G., M. van ALBADA, H. APPELMAN and P. UBBELS, Het verband tussen de eikwaliteit en de broeduitkomsten. *Tijdschrift voor Diergeneeskunde* 77, 825-838, 1952. 90, 91
- BRODY, S., Growth and development with special reference to domestic animals. IV. Growth rates during the self-accelerating phase of growth. *Missouri-Agricultural Experiment Station Research Bulletin* 98, 1927. 200

- BRONKHORST, J. J., A physical, chemical and physiological study of high and low hatching lines of single comb White Leghorns. Ph.D. Thesis Cornell University (Ithaca, N.Y.), 1933. 90, 117, 134, 179, 181-183, 186, 188, 197-199
- BRONKHORST, J. J., and G. O. HALL, Hatchability studies. I. The physiology and chemistry of the blood of high and low hatching lines. *Poultry Science* 14, 42-45, 1935 a. 134
- BRONKHORST, J. J. and G. O. HALL, Hatchability studies. II. A physical study of eggs from high and low hatching hens. *Poultry Science* 14, 112-115, 1935 b. 90
- BROWN, E., Practical Artificial Incubation. 2nd ed. London, Paris and New York (Cassell, Petter, Galpin & Co.), 1881. 44
- BROWN, W. O., Liver meal as a riboflavin supplement for breeding hens. *Journal of the Science of Food and Agriculture* 2, 43-46, 1951. 95
- BROWN, W. O., Effect of diet on the serum riboflavin of the laying hen. *Nature* 169, 454-455, 1952. 95
- BRUNSON, C. C., G. F. GODFREY and B. L. GOODMAN, Heritability of all-or-none traits: hatchability and resistance to death to ten weeks of age. *Poultry Science* (Abstract 34, 1183, 1955), 35, 516-523, 1956. 181, 183
- BRUYERIN, J. B., Io. Bruyerino Campegio De Re Cibaria Libri XXII. Lugduni (Sebast. Honoratvm), 1540. 17, 21
- BRYANT, R. L. and P. F. SHARP, Effects of washing on the keeping quality of hens' eggs. *Journal of Agricultural Research* 48, 67-89, 1934. 85
- BUCHANAN, J. W., Regional differences in rate of oxidations in the chick blastoderm as shown by susceptibility to hydrocyanic acid. *Journal of Experimental Zoology* 45, 141-157, 1926. 196
- BUCKNELL, W., The Eccleabion; a Treatise on Artificial Incubation. London, 1839.
- BUCKNER, G. D., J. H. MARTIN and A. M. PETER, The relation of calcium restriction to the hatchability of eggs. *American Journal of Physiology* 71, 543-547, 1924-1925. 87
- BUCKNER, G. D., J. H. MARTIN and A. M. PETER, Calcium metabolism in the laying hen. III. Calcium carbonate and hatchability. *Kentucky Agricultural Experiment Station Bulletin* 291, 1929. 87
- BURKE, E., A study of incubation. *Montana Agricultural Experiment Station Bulletin* 178, 1925. 55
- BURNS, C. H., L. E. BROWNELL and H. C. ECKSTEIN, Wholesomeness of a gamma-irradiated diet fed to chickens. *Federation Proceedings* 15, 910-917, 1956. 106
- BUSHNELL, L. D., W. R. HINSHAW and L. F. PAYNE, Bacillary white diarrhea in fowl. *Kansas Agricultural Experiment Station Technical Bulletin* 21, 1926. 200
- BUSS, E. G., Some factors which affect hatchability of chicken eggs at higher altitudes. Ph.D. Thesis, Purdue University, 1956 (University Microfilms Mic. 56-2773). 62
- BUSS, E. G., R. V. BOUCHER and A. J. G. MAW, Physiological characteristics associated with a mutant gene in chickens that causes a deficiency of riboflavin. 1. Eggs and embryos. (Abstract). *Poultry Science* 38, 1192, 1959. 97
- BUZA, L., Adatok a csirkeembriók torzfejlődéséhez és hibás fejlődéséhez (Malformations and defective formations of chicken embryos). *Magyar Állatorvosok Lapja* 1958, pp. 200-203. 202
- BYERLY, T. C., The effect of breed on the growth of the chick embryo. *Journal of Morphology and Physiology* 50, 341-359, 1930. 178

- BYERLY, T. C., Time of occurrence and probable causes of mortality in chick embryos. Report of Proceedings of the 4th World's Poultry Congress at the Crystal Palace, London, England: July 22-30, 1930, pp. 178-183, 1931.
- BYERLY, T. C., Some factors affecting the length of the incubation period. Atti del V. Congresso Mondiale di Pollicoltura tenutosi in Roma dal 6 al 15 Settembre 1933 2, 373-379, 1934. 73, 188, 198
- BYERLY, T. C., Effect of different incubation temperatures on mortality of chick embryos. Poultry Science 17, 200-205, 1938. 192, 199
- BYERLY, T. C. and S. K. HAYNES, Testing eggs prior to incubation. Poultry Science 17, 152-154, 1938. 91
- BYERLY, T. C. and M. A. JULL, "Stickiness" a lethal factor in the domestic fowl. Journal of Experimental Zoology 62, 489-498, 1932. 164, 166
- BYERLY, T. C. and M. A. JULL, Sex ratio and embryonic mortality in the domestic fowl. Poultry Science 14, 217-220, 1935. 170
- BYERLY, T. C., C. W. KNOX and M. A. JULL, Some genetic aspects of hatchability. Poultry Science 13, 230-238, 1934. 179
- BYERLY, T. C. and M. W. OLSEN, The influence of gravity and air-hunger on hatchability. Poultry Science 10, 281-287, 1930-1931. 62, 191
- BYERLY, T. C. and M. W. OLSEN, Time and manner of determination of the malposition head-in-small-end of egg. Poultry Science (Abstract 11, 369, 1932) 12, 261-265, 1933. 191
- BYERLY, T. C. and M. W. OLSEN, Causes of the embryonic malposition head-under-left-wing. Poultry Science 13, 278-282, 1934. 191, 192
- BYERLY, T. C. and M. W. OLSEN, Lethality of embryo malpositions in the domestic fowl. Poultry Science 15, 158-162, 1936 a. 191
- BYERLY, T. C. and M. W. OLSEN, Certain factors affecting the incidence of malpositions among embryos of the domestic fowl. Poultry Science 15, 163-168, 1936 b. 190-192
- BYERLY, T. C. and M. W. OLSEN, Egg turning, pipping position and malpositions. Poultry Science 16, 371-373, 1937. 191, 192
- BYERLY, T. C., H. W. TITUS and N. R. ELLIS, Production and hatchability of eggs as affected by different kinds and quantities of proteins in the diet of laying hens. Journal of Agricultural Research 46, 1-22, 1933 a. 111, 118, 119
- BYERLY, T. C., H. W. TITUS, and N. R. ELLIS, Effect of diet on egg composition. II. Mortality of embryos in eggs from hens on diets containing protein supplements of different origin. Journal of Nutrition 6, 225-242, 1933 b. 108, 111
- BYERLY, T. C., H. W. TITUS, N. R. ELLIS and W. LANDAUER, A new nutritional disease of the chick embryo. Proceedings of the Society for Experimental Biology and Medicine 32, 1542-1546, 1935. 111
- BYERLY, T. C., H. W. TITUS, N. R. ELLIS and R. B. NESTLER, Effects of light, soybeans and other diet supplements on seasonal hatchability and egg production. Poultry Science 16, 322-330, 1937.
- CADMAN, W. H., Egyptian incubators and methods of incubation. Transactions of the First World's Poultry Congress at the Hague-Scheveningen, September 5-9, 1921, 2, 97-105. 19
- CALL, V. D. and H. L. WILCKE, Effect of single cereal grains upon the hatchability of eggs and subsequent growth of chicks. Poultry Science 18, 308-317, 1939. 108
- CALLENBACH, E. W. and C. A. HILLER, The artificial propagation of ring-necked pheasants. Pennsylvania Agricultural Experiment Station Bulletin 299, 1933. 60
- (CAMPBELL, J.), The Travels and Adventures of Edward Brown, Esq.; formerly a Merchant in London. London (J. Applebee), 1739. 19

- CANEVAZZI, O., Ricerche sulla distribuzione ed utilizzazione, da parte dell'embrione di pollo, del glucosio introdotto artificialmente nell'uovo, in condizioni sperimentali diverse. *Archivio Italiano di Anatomia e di Embriologia* 43, 187-210, 1940. 56
- CANFIELD, H., The effects of bacillary white diarrhea. *Michigan Agricultural Experiment Station Quarterly Bulletin* 8, 31-32, 1925. 200
- CANTELO, W. J., A practical exposition of the Cantelonian system of hatching eggs, and rearing poultry, game, etc., by hydro-incubation, or top-contact heat. 3rd edition. London (William Strange), 1849. 44
- CARBONNIER, P., Observations faites sur l'incubation des oeufs de Gallinacés. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 68, 613-615, 1869.
- CARD, L. E., Incubator eggs turned first six days hatch well. *Thirty-ninth Annual Report Illinois Agricultural Experiment Station for year ended June 30, 1926.* 63
- CARD, L. E., Vitamin E requirements of poultry. *Poultry Science* 8, 328-334, 1928-1929. 106
- CARD, L. E., The effect of soybean meal on hatchability. *Poultry Science* 21, 467, 1942. 109
- CARD, L. E., H. H. MITCHELL and T. S. HAMILTON, Further studies on the vitamin E requirements of poultry. II. The performance of pullets raised on a vitamin E free diet. *Proceedings of the Twenty-second Annual Meeting, Poultry Science Association, Macdonald College, Quebec, Canada, July 9-11, 1930, pp. 29-31.* 106, 107
- CARDANUS, Hieronymi Cardani Operum Tomvs Tertivs; qvo continentvr Physica. Lvgdvni (Ioannis Antonii Hvgvetan & Marci Antonii Ravavd), 1663. 19
- CARDWELL, J., Artificial incubation in Egypt. Reports from the Consuls of the United States, issued from the Bureau of Statistics, Department of State 33, 502-508, 1890 (also issued as House Miscellaneous Document No. 267, 51st Congress 1st Session. Reprinted in: *Scientific American Supplement* 30, 12431-12432, 1890). 19
- CARLSON, C. W., Effects of antibacterial and antifungal agents in diets for laying and breeding hens. *South Dakota Agricultural Experiment Station Technical Bulletin* 22, 1959 (Abstract: *Poultry Science* 35, 1136, 1956). 101
- CARLSON, C. W., R. A. WILCON, W. KOHLMAYER and D. G. JONES, Reproductive performance of chickens as influenced by antibiotics in the diet. *South Dakota Agricultural Experiment Station Technical Bulletin* 15, 1955.
- CARNE, H. R. and W. L. WATERHOUSE, Sex-reversal and abnormal sex ratios in the domestic fowl. *Journal of Heredity* 49, pp. 102 and 106, 1958. 171
- CARR, J. G., Lack of transmission of avian tumour virus from carrier hens to their offspring via the egg. *Proceedings of the Royal Society of Edinburgh, Section B* 62, 54-58, 1943-1944. 202
- CARVER, J. S. and J. MCGINNIS, Effect of an "animal protein factor" fermentation product on hatchability of chicken eggs. *Poultry Science* 29, 307-309, 1950. 100
- CARVER, J. S. and J. MCGINNIS, Effect of vitamin B₁₂ and APF supplements on hatchability of chicken eggs. Abstract, *Poultry Science* 29, 752, 1950. 100
- CARVER, J. S., J. MCGINNIS, C. F. McCLARY and R. J. EVANS, The utilization of raw and heat treated soybean oil meal for egg production and hatchability. Abstract. *Poultry Science* 25, 399, 1946. 109
- CARVER, J. S., E. I. ROBERTSON, D. BRAZIE, R. H. JOHNSON and J. L. ST. JOHN, The vitamin D requirements of chickens. *Washington Agricultural Experiment Station Bulletin* 299, 1934. 103

- CASKEY, C. D., L. C. NORRIS and G. F. HEUSER, A chronic congenital ataxia in chicks due to manganese deficiency in the maternal diet. *Poultry Science* 23, 516-520, 1944. 111
- CAVE, C. J. P. and T. V. JONES, Artificial incubation. *Nature* 115, 498, 1925. 60
- CAVERS, J. R. and F. B. HUTT, The relation between abnormal orientation of the 4-day embryo and position of the chick at hatching. *Journal of Agricultural Research* 48, 517-531, 1934. 191
- CEDERHJELM, C. W., Försök af kycklinge - kläckning uti ugnar gjorde. *Kongl. Svenska Vetenskaps Academiens Handlingar* 9, 251-264, 1748. 37, 38
- CHAMPION, J., Hatching eggs and rearing young birds. *Champion's Specification*. His Majesty's High Court of Chancery, Specification No. 950, 1770. 42
- CHAMPION, L. R., Studies in hatchability. I. Effect of backcrossing first generation females produced by reciprocal strain classes of Leghorns. *Quarterly Bulletin, Michigan Agricultural Experiment Station* 37, 307-315, 1955. 175
- CHAMPION, L. R., Studies in hatchability. II. The performance of two strains of Leghorns in inter and intra-strain matings. *Quarterly Bulletin, Michigan Agricultural Experiment Station* 39, 321-326, 1956. 175
- CHAMPION, L. R., Studies in hatchability. III. Effects of backcrossing inter-strain Leghorns. *Quarterly Bulletin, Michigan Agricultural Experiment Station* 39, 457-468, 1957. 181
- CHAMPION, L. R., Sex ratio in two strains of Leghorns and their reciprocal crosses. *Poultry Science* 39, 876-881, 1960. 170
- CHATTOCK, A. P., Moisture and incubation. *Transactions of the First World's Poultry Congress at the Hague-Scheveningen, September 5-9, 1921*, 1, 37-47.
- CHATTOCK, A. P., On the physics of incubation. *Philosophical Transactions of the Royal Society of London, B* 213, 397-450, 1925. 63
- CHEVALLIER, A., Note sur l'incubation artificielle de Chaudes-Aigues. *Journal des connaissances usuelles et pratiques* 13, 98, 1831. 43
- CHIN, D., J. B. ANDERSON, R. F. MILLER, L. C. NORRIS and G. F. HEUSER, The vitamin B₁₂ requirements of White Leghorn hens. *Poultry Science* 37, 335-343, 1958. 101
- CHOLEVČUK, M., Influence des rayons ultraviolets sur l'éclosion des poulets. *Comptes Rendus de la Société de Biologie* 100, 586-587, 1929. 105
- CHOLEVČUK, M., Wirkung der Quarzlampe auf Eier und Hühner. *Biol. Listy* 14, 1929 (In Czech.) German abstract in *Berichte über die wissenschaftliche Biologie* 12, 474, 1929. 105
- CHOMEL, Dictionnaire oeconomique or, The Family Dictionary. Done into English from the Second Edition, lately printed at Paris, in two volumes, folio, written by M. Chomel: with considerable alterations and improvements, revised and recommended by Mr. R. Bradley. London (D. Midwinter), 1725. 19
- CHRISTIANSEN, J. B., J. G. HALPIN and E. B. HART, A possible relation between manganese, sunlight and winter hatchability of hen's eggs. *Science* 90, 356-357, 1939. 112
- CHRISTIANSEN, J. B., J. G. HALPIN and E. B. HART, Studies on the nature of the effective supplements for soybean oil meal in rations for the production of hatching eggs. *Poultry Science* 19, 55-60, 1940.
- CHRISTY, T., *Hydro-Incubation: its Theory and Practice*. 7th edition. London (Christy and Co.), 1881. 44
- CHUBB, L. G., Further observations on the feeding of manganese deficient diets to growing and breeding chickens. Report of Proceedings, Tenth World's Poultry Congress Edinburgh, Scotland 13th-21st August, 1954. Part II, Section papers, pp. 164-166, 1954. 112

- CLARK, T. B. and C. J. CUNNINGHAM, Soybean oil meal in poultry rations. West Virginia Agricultural Experiment Station Bulletin 325, 1945. 109
- COATES, M. E., M. K. DAVIES and G. F. HARRISON, Antivitamin B₁₂ activity for the growing chick and developing chick embryo of some analogs of cyanocobalamin. Archives of Biochemistry and Biophysics 87, 93-99, 1960. 101
- COCHEZ, L. P., An infertility factor balanced by breeding in the White Wyandotte. IXth World's Poultry Congress Paris 1951, Official Reports 1, 122-128. 138
- COLASANTI, G., Über den Einfluss der Kälte auf die Entwicklungsfähigkeit des Hühneries. Archiv für Anatomie, Physiologie und wissenschaftliche Medizin 1875, pp. 477-479. 51
- COLASANTI, G., L'influenza dell' abbassamento di temperatura sullo sviluppo dell' uovo di gallina. Atti della R. Accademia dei Lincei, series 2, 2, 543-544, 1874-1875 (Identical with preceding). 51
- COLE, L. J. and J. G. HALPIN, Preliminary report of an experiment on close inbreeding in fowls. Journal of the American Association of Instructors and Investigators in Poultry Husbandry 3, 7-8, 1916. 172
- COLE, L. J. and J. G. HALPIN, Results of eight years of inbreeding Rhode Island Reds. Anatomical Record 23, 97, 1922. 172
- COLE, R. K., A new autosomal lethal in the fowl. Poultry Science 18, 403-404, 1939. 143
- COLE, R. K., The "talpid lethal" in the domestic fowl. Journal of Heredity 33, 83-86, 1942. 143, 145, 161
- COLES, R., Some observations on breeding fowl resistant to lymphomatosis. Poultry Science 34, 312-322, 1955. 203
- COLES, R., Observations on the occasional depressing influence of fish meal on the hatchability of hens' eggs. Journal of Agricultural Science 47, 354-362, 1956 a. 111
- COLES, R., The influence of the hen's egg weight on hatching. Poultry Science 35, 817-822, 1956 b. 68
- COLES, R., Primary and secondary sex ratios in domestic fowl. Empire Journal of Experimental Agriculture 21, 167-177, 1956 c. 171
- COLES, R. and F. CUMBER, Observations on the relationship between riboflavin, hatchability and clubbed down. Journal of Agricultural Science 46, 191-198, 1955. 95
- COLES, R. and F. CUMBER, The relationship between fertility, hatchability and mortality in fowl. British Veterinary Journal 112, 491-496, 1956. 197
- COLES, R. and J. R. UNDERWOOD, Hatchability of hen eggs and lymphomatosis. Nature 173, 877-878, 1954 a. 203
- COLES, R. and J. R. UNDERWOOD, Some observations on hatching rates in hens' eggs. Empire Journal of Experimental Agriculture 22, 281-292, 1954 b. 118
- COLLINS, W. M. and W. HUBBARD, Influence of plumage color on hatching ratio and growth rate in chickens. Poultry Science 37, 69-77, 1958. 164
- COLUMELLA, LUCIUS IUNIUS MODERATUS, Res Rustica. On Agriculture. English translation by E. S. Forster and E. H. Heffner. Vol. 2. Loeb Classical Library. Cambridge (Harvard University Press), 1954. 49
- COONEY, W. T., Preincubation humidity variation effects on chicken egg hatchability. Oregon Agricultural Experiment Station Technical Bulletin 2, 1943. 51
- COOPER, D. M. and J. G. ROWELL, Relations between fertility, embryonic survival and some semen characteristics in the chicken. Poultry Science 37, 699-707, 1958. 128

- COOPER, D. M. and G. SKULSKI, Effect of feeding 2-amino-5-nitrothiazole and 2-acetyl-amino-5-nitrothiazole on reproduction in the fowl. *Journal of Comparative Pathology and Therapeutics* 67, 186-193, 1957.
- (COPINEAU), Ornithotrophie artificielle ou art de faire éclore et d'élever la volaille par le moyen d'une chaleur artificielle. Paris (Benoît Morin), 1780. 41
- (COPINEAU), Art de faire éclore et d'élever la volaille par le moyen d'une chaleur artificielle. Paris, 1783. 41
- (COPINEAU), L'Homme rival de la nature ou l'Art de faire éclore et d'élever la volaille par le moyen d'une chaleur artificielle. Paris, an III (1795). 41
- (COPINEAU), L'Art de faire éclore la volaille au moyen d'une chaleur artificielle par Réaumur, corrigé par l'abbé***. Paris, an VII (1799). 41
- CORBETT, A., How to Hatch and Raise Every Kind of Poultry with the Aid of Manure. Hempsted, L.L., 1874 (Chinese edition, preface dated 1894: Nung-hsüeh ts'ung-shu. Shanghai nung-hsüeh hui. Shanghai). 24, 39
- CORBETT, A., The Poultry Yard and Market; a Practical Treatise on Gallinoculture, and Description of a New Process for Hatching Eggs and Raising Poultry by Means of Horse Manure. New York (Orange Judd Company), 1876. 24, 39
- COUCH, J. R., W. W. CRAVENS, C. A. ELVEHJEM and J. G. HALPIN, Biotin deficiency in the newly hatched chick. Abstract. *Poultry Science* 26, 536, 1947. 99
- COUCH, J. R., W. W. CRAVENS, C. A. ELVEHJEM and J. G. HALPIN, Relation of biotin to congenital deformities in the chick. *Anatomical Record* 100, 29-48, 1948 a. 99, 194
- COUCH, J. R., W. W. CRAVENS, C. A. ELVEHJEM and J. G. HALPIN, Relation of carbohydrate to intestinal synthesis of biotin and hatchability in mature fowl. *Journal of Nutrition* 35, 57-72, 1948 b. 100
- COUCH, J. R., W. W. CRAVENS, C. A. ELVEHJEM and J. G. HALPIN, Studies on the role of biotin in embryonic development of the domestic fowl. Abstract, *Poultry Science* 27, 657, 1948c.
- COUCH, J. R., W. W. CRAVENS, C. A. ELVEHJEM and J. G. HALPIN, Studies on the function of biotin in the domestic fowl. *Archives of Biochemistry* 21, 77-86, 1949. 99
- COUCH, J. R., J. F. FLAM and L. L. GEE, Effect of penicillin on growth, egg production and hatchability. *Federation Proceedings* 10, 379, 1951.
- COUCH, J. R. and H. L. GERMAN, Pteroylglutamic acid studies with the mature fowl. *Poultry Science* 29, 539-544, 1950. 99
- COUCH, J. R., H. L. GERMAN and P. B. PEARSON, Pteroylglutamic acid studies with mature domestic fowl. (Abstract) *Poultry Science* 28, 761-762, 1949. 99
- COUCH, J. R., L. E. JAMES and R. M. SHERWOOD, The effect of different levels of manganese and different amounts of vitamin D in the diet of hens and of pullets. *Poultry Science* 26, 30-37, 1947. 103, 112
- COUCH, J. R., O. OLCESE, B. G. SANDERS and J. V. HALICK, Vitamin B₁₂, APF concentrates, dried whey, fish solubles and liver fraction "L" in the nutrition of the mature fowl. *Journal of Nutrition* 42, 473-485, 1950. 100
- CRAMPTON, L. R., Studies in hatchability. I. Effects of backcrossing first generation females produced by reciprocal strain crosses of Leghorns. *Quarterly Bulletin Michigan Agricultural Experiment Station* 37, 307-315, 1955. 175
- CRAVENS, W. W., The effect of leucine on egg production and hatchability. *Poultry Science* 27, 562-570, 1948. 110
- CRAVENS, W. W. and J. R. COUCH, Relation of carbohydrate to intestinal synthesis of biotin and hatchability in mature fowl. *Federation Proceedings* 6, 404, 1947. 100

- CRAVENS, W. W. and J. G. HALPIN, The effect of pteroylglutamic acid and an unidentified factor on egg production and hatchability. *Journal of Nutrition* 37, 127-138, 1949.
- CRAVENS, W. W., J. G. HALPIN and W. H. MCGIBBON, The use of various vitamin supplements in rations for laying and breeding hens. *Poultry Science* 25, 99-104, 1946. 97
- CRAVENS, W. W. and C. E. HOLMES, The effect of alfalfa leaf meal and dried cereal grass on hatchability and egg production. Abstract. *Poultry Science* 20, 458, 1941.
- CRAVENS, W. W., C. E. HOLMES, J. G. HALPIN and C. A. ELVEHJEM, The effect of alfalfa leaf meal and dried cereal grass on egg production and hatchability. *Poultry Science* 21, 301-305, 1942.
- CRAVENS, W. W., W. H. MCGIBBON and E. E. SEBESTA, Effect of biotin deficiency on embryonic development in the domestic fowl. *Anatomical Record* 90, 55-64, 1944. 99, 194, 195
- CRAVENS, W. W., E. E. SEBESTA, J. G. HALPIN, and E. B. HART, Effect of biotin on reproduction in the domestic fowl. *Proceedings of the Society for Experimental Biology and Medicine* 50, 101-104, 1942 a. 99
- CRAVENS, W. W., E. E. SEBESTA, J. G. HALPIN, and E. B. HART, Effect of *Lactobacillus casei* E eluate fraction on reproduction in the domestic fowl. *Proceedings of the Society for Experimental Biology and Medicine* 51, 106-108, 1942 b. 99
- CRAVENS, W. W., E. E. SEBESTA, J. G. HALPIN, and E. B. HART, Effect of vitamin B₆ on egg production and hatchability. *Poultry Science* 22, 94-95, 1943. 98
- CRAVENS, W. W., E. E. SEBESTA, J. G. HALPIN and E. B. HART, Studies on the pyridoxin requirements of laying and breeding hens. *Poultry Science* 25, 80-82, 1946. 98
- CRAVENS, W. W. and E. E. SNELL, Desoxypyridoxine and development of the chick embryo. *Federation Proceedings* 8, 380-381, 1949a. 98
- CRAVENS, W. W. and E. E. SNELL, Effects of desoxypyridoxine and vitamin B₆ on development of the chick embryo. *Proceedings of the Society for Experimental Biology and Medicine* 71, 73-76, 1949b. 98
- CREGER, C. R., M. E. HAQUE, R. E. DAVIES and J. R. COUCH, Reproduction studies in the mature fowl. (Abstract). *Poultry Science* 38, 1196, 1959.
- CRESCENZI, Petri de crescentijs ciuis Bononiensis epistola in librū comodorū ruralium. Augsburg (iohannē Schüzler), 1471. 19
- CREW, F. A. E., On fertility in the domestic fowl. *Proceedings of the Royal Society of Edinburgh* 46, Part II, 230-237, 1925-1926. 128
- CREW, F. A. E., *Animal Genetics*. Edinburgh (Oliver and Boyd), 1926.
- CREW, F. A. E., The sex ratio of the domestic fowl and its bearing upon the sex-linked lethal theory of differential mortality. *Proceedings of the Royal Society of Edinburgh*, 58, Part I, 73-79, 1938. 170
- CRITTENDEN, L. B., Factors affecting the efficiency of selection for hatchability. Ph.D. thesis Purdue University 1958. University Microfilms 58-1771. 183
- CRITTENDEN, L. B., B. B. BOHREN and V. L. ANDERSON, Genetic variance and covariance of the components of hatchability in New Hampshires. *Poultry Science* 36, 90-103, 1957 a. 181, 183
- CRITTENDEN, L. B., B. B. BOHREN and V. L. ANDERSON, A comparison of different criteria of selection for hatchability in chickens. *Poultry Science* 36, 104-110, 1957 b.
- CROSS, L. J., A study of the relation of the chemical composition of the hens' eggs to the vitality of the young chick. Thesis, Cornell University, 1912. 91

- CROUCH, N., A Strange and True Account of the Late Travels of Two English Pilgrims, and what Admirable Accidents befell them in their journey to Jerusalem, Grand Cairo, Alexandria, etc. In a letter from H. T. In: Two Journeys to Jerusalem. Collected by R. B. London (N. Crouch), 1704 (first edition 1683). 19
- CROWTHER, J. G., The Social Relations of Science. New York (Macmillan Company), 1941. 46
- CRUICKSHANK, F. M., The effect of diet on the chemical composition, nutritive value and hatchability of the egg. Nutrition Abstracts and Reviews 10, 645-654, 1941.
- CRUZ, S. R. and A. L. ROMANOFF, Effect of oxygen concentration on the development of the chick embryo. Physiological Zoology 17, 184-187, 1944. 67
- CSONKA, F. A., M. W. OLSEN and J. R. SZMOR, Chick embryonic death in relation to maternal diet. Federation Proceedings 13, 195, 1954.
- CULTON, T. C., T. L. CLIFFORD and J. R. SMYTH, Supplementary effect of certain plant and animal feedstuffs and crystalline vitamins to rations composed of plant feedstuffs. Abstract. Poultry Science 26, 536-537, 1947.
- CUNNINGHAM, B., The incubation of hen eggs under increased atmospheric pressure. Journal of the Elisha Mitchell Scientific Society 42, 188-192, 1927. 64
- CUNNINGHAM, B., The effect of humidity on the developmental rate of chick embryos incubated under increased atmospheric pressure. Science 87, 90-91, 1938. 64
- CUPR, Ueber Reaumur's Versuche der künstlichen Ausbrütung der Eier mittelst der Düngerwärme. Sitzungsberichte der königl. böhmischen Gesellschaft der Wissenschaften in Prag 1866, pp. 18-19.
- CUTLER, I. E., Reptilian fowls. Journal of Heredity 16, 352-356, 1925. 138
- CYPHERS, C. A., Incubation and its Natural Laws. Third edition. 1894.
- CZARNECKA, J., Ciężar jaj i ich zdolność wylęgowa. Przegląd Hodowlany 1954, pp. 40-44. 68
- DABRY, P., Sur l'incubation artificielle en Chine. Bulletin mensuel de la Société impériale zoologique d'acclimatation 2^e série 2, 394-400, 1865. 10
- DANFORTH, C. H., Artificial and hereditary suppression of sacral vertebrae in the fowl. Proceedings of the Society for Experimental Biology and Medicine 30, 143-145, 1932.
- DANFORTH, C. H., *Gallus sonnerati* and the domestic fowl. Journal of Heredity 49, 167-169, 1958. 168
- DARESTE, C., Recherches sur la production des monstres, dans l'oeuf de la poule, par l'effet de l'incubation tardive. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 95, 254-256, 1882. 48
- DARESTE, C., Nouvelles recherches sur la production des monstres, dans l'oeuf de la poule, par l'effet de l'incubation tardive. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 96, 444-446, 1883 a. 48
- DARESTE, C., Recherches sur la production des monstruosités par les secousses imprimées aux oeufs de poule. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 96, 511-513, 1883 b. 53
- DARESTE, C., Nouvelles recherches concernant l'influence des secousses sur le germe de l'oeuf de poule, pendant la période qui sépare la ponte de la mise en incubation. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 101, 834-836, 1885. 53
- DARESTE, C., Détermination des conditions physiologiques et physiques de l'évolution normale de l'embryon de la poule. Association Française pour l'Avancement des Sciences. Compte Rendu de la 15^e session, Nancy 1886, 554-566, 1887. 48

- DARESTE, C., Recherches sur la production artificielle des monstruosités ou essais de tératogénie expérimentale. 2nd ed. Paris (C. Reinwald et Cie.) 1891. For further references see *Dareste* (1887) or *Strong* (1939). 53
- DAVIS, G. I., Influence of oxygen concentration on hatchability and on selecting for hatchability. *Poultry Science* 34, 107-113, 1955. 62
- DAVIS, H. J., L. C. NORRIS and G. F. HEUSER, The vitamin G requirements of laying hens. Abstract. *Poultry Science* 15, 427-428, 1936.
- DAVIS, H. J., L. C. NORRIS and G. F. HEUSER, The rôle of vitamin G in reproduction in poultry. *Poultry Science* 17, 81-86, 1938a. 94
- DAVIS, H. J., L. C. NORRIS and G. F. HEUSER, Further evidence on the amount of vitamin G required for reproduction in poultry. *Poultry Science* 17, 87-93, 1938b. 94, 97
- DAVIS, H. J. and C. W. UPP, Studies on the fat requirement of the domestic fowl. Abstract. *Poultry Science* 20, 459, 1941.
- DAVY, J., Some observations on incubation. *Proceedings of the Royal Society of Edinburgh* 5, 642-643, 1866.
- DAY, W. H., Humidity in relation to incubation. *Ontario Agricultural College Bulletin* 163, 29-50, 1908.
- DEAKIN, A. and G. ROBERTSON, Effect of mercurial ointment on hatchability. *Poultry Science* 12, 378-381, 1933.
- DEAN, W. F. and E. L. STEPHENSON, The influence of dietary furazolidone on egg production, hatchability, fertility, and feed efficiency of laying and breeding hens. *Poultry Science* 37, 124-128, 1958. 111
- DEARSTYNE, R. S., B. F. KAUPP and H. S. WILFONG, Study of pullorum disease from a flock standpoint. *North Carolina Agricultural Experiment Station Technical Bulletin* 36, 1929. 200
- DELAPYLAIE, Rapport sur une visite à l'incubation des oeufs par le calefacteur-couvoir. *Journal des connaissances usuelles et pratiques* 10, 4-6, 1829.
- DELPECH et COSTE, Recherches sur la formation des embryons des oiseaux. In: *Recherches sur la génération des mammifères par M. Coste. Suivies de recherches sur la formation des embryons par MM. Delpech et Coste.* Paris (J. Rouvier et E. Le Bouvier), 1834. 44, 45
- DELUC, J. A., Copie d'un Mémoire sur un hygrometre comparable. *Journal de Physique* 5, 381-397, 1775. 41
- DELUC, J. A., Suite d'un mémoire sur un hygrometre comparable. *Journal de Physique* 5, 457-476, 1775. 41
- DEMOCRITUS in: *Constantini Caesaris selectarum praeceptionum de agricultura libri viginti, Iano Cornario medico physico interprete, recens in lucem emissi.* Venetia, 1538. Translation: *Geoponika. Agricultural Pursuits.* Translated from the Greek by the Rev. T. Owen. London, 1805. 24, 25
- DEMUTH, F., Über die Beziehungen des Energiestoffwechsels zu Wachstum und Differenzierung. II. Die Wirkung von Sauerstoff auf Wachstum und Entwicklung von Hühnerembryonen. *Proceedings, Koninklijke Nederlandsche Akademie van Wetenschappen* 42, 506-514, 1939. 189
- DERANIYAGALA, P. E. P., Hybridization in the jungle fowl of Ceylon. *Spolia Zeylanica* 27, 59-61, 1953. 169
- DERANIYAGALA, P. E. P., Growth, subspeciation and hybridisation in the Ceylon Jungle Fowl *Gallus lafayetti*. *Spolia Zeylanica* 28, 99-106, 1956. 169
- DEUCHAR, E. M., The effect of a high temperature shock on early morphogenesis in the chick embryo. *Journal of Anatomy* 86, 443-458, 1952. 55
- DEVAUX, P., L'incubation artificielle. *La Nouvelle Revue* 77, 564-582, 1892. 28

- DHARMARAJAN, M., Effect on the embryo of staleness of the sperm at the time of fertilization in the domestic hen. *Nature* 165, 398, 1950. 128, 130
- DIECKERT, J. W., S. O. BROWN and J. R. COUCH, A study of the effect of a biotin deficient diet on the embryonic development of chicks. Abstract. *Poultry Science* 29, 756, 1950.
- DIECKERT, J. W., and J. R. COUCH, The liver "L" hatchability factor in the nutrition of mature fowl (Abstract). *Poultry Science* 30, 935, 1951.
- DIGBY, K., Of Bodies, and of Mans Soul. To Discover the Immortality of Reasonable Souls. London (John Williams), 1669. 36
- DIODORUS SICULUS, The Historical Library of Diodorus the Sicilian. Made English by G. Booth. London (Awnshem and J. Churchill and E. Castle), 1700. 17, 20, 23
- DMITRIEVA, E. V., The influence of the vitamin D on the productivity of adult hens. Comparative efficiency of irradiated yeast and cod liver oil on the productivity of the hen and the incubatory quality of the egg. *Transactions on the Dynamics of Development* 9, 303-310, 1935. 105
- DMITRIEVA, H. W., Thymus and viability. I. Weight of the thymus in the chick embryo. *Bulletin de Biologie et de Médecine Expérimentale de l'URSS* 8, 35-36, 1939. 189, 190
- DOLS, M. J. L., The influence of Vitamin E on hatchability. *Archives Néerlandaises de Physiologie de l'homme et des animaux* 22, 372-381, 1937. 107
- DOUGHERTY, J. E., Studies in incubation. I. The effect of low temperature previous to incubation on hatchability of eggs set. *American Journal of Physiology* 79, 39-43, 1926-1927. 51
- DOUSA, J., Cornelis Drebbel. Notes and Queries 1st series, 2, 6-7, 1850. 29
- DOVE, W. F., Classification of chick-embryo positions at different ages and malpositions as a cause of mortality. *Journal of Agricultural Research* 50, 923-931, 1935 a. 190, 192
- DOVE, W. F., 1935 b quoted by Hays (1941). 171
- DREBBEL, C., Manuscript 2206, Ll. V. 8, Part II, I, pp. 170-171. University Library Cambridge. Title of manuscript: A very Good Collection of Approved Receipts of Chymical operations Collected by Augustus Kuffler and Charles Ferrers Phylchymist; dated 1666-1690. Text of "The Description of two Furnaces, etc." reprinted (without figures) in Jaeger (1922). 28-31
- DRIMMELEN, G. C. VAN, Die verhouding tussen vrugbaarheid en uitkombaarheid van hoenderciers. *South African Science* 1, 187-189, 1948.
- DRYDEN, J., Poultry experiments. *Utah Agricultural Experiment Station Bulletin* 102, 1907. 58, 65
- DRYDEN, J., Incubation experiments. *Oregon Agricultural Experiment Station Bulletin* 100, 1908. 5, 58
- DUDLEY, F. J., Results of crossing the Rhode Island Red and White Leghorn breeds of poultry. *Journal of Agricultural Science* 34, 76-81, 1944. 179
- DUDLEY, F. J. and W. L. S. HINDHAUGH, Sex ratios and comparative rearability of the sexes in the cross-breeding experiment (1934-7) at the Northern Breeding Station of the National Poultry Institute, Reaseheath. *Journal of Genetics* 37, 491-497, 1938-1939. 170
- DUMON, A. G., The effects of inbreeding on hatchability. Report of Proceedings of the 4th World's Poultry Congress at the Crystal Palace, London, England: July 22-30, 1930, 1-5, 1931. 174, 176
- DUMON, A. G., La sélection généalogique et consanguine de la poule pondeuse (Leghorn). *Agricultura (Louvain)* 41, 11-41, 1938. 174, 176

- DUNAHOO, W. S., H. M. EDWARDS, JR., S. C. SCHMITTLE and H. L. FULLER, Studies on toxic fat in the rations of laying hens and pullets. *Poultry Science* 38, 663-667, 1959. 110
- DUNKERLY, J. S., The effect of inbreeding. Report of Proceedings of the 4th World's Poultry Congress, London, England 1930, 46-68, 1931. 174
- DUNN, L. C., Hatchability and chick mortality. *Poultry Science* 1, 33-38, 1921-1922. 197
- DUNN, L. C., The relationship between the weight and the hatching quality of eggs. Storrs Agricultural Experiment Station Bulletin 109, 1922. 67, 72
- DUNN, L. C., The variation of eggs in the rate at which they lose weight. Part I. *Poultry Science* 2, 45-58, 1922-1923. Part II. *Ibid.*, 166-171. Part III. *Ibid.*, 199-204. 76, 77
- DUNN, L. C., A lethal gene in fowls. *American Naturalist* 57, 345-349, 1923 a. 137
- DUNN, L. C., Experiments on close inbreeding in fowls. Storrs Agricultural Experiment Station Bulletin 111, 1923 b. 171-174
- DUNN, L. C., The problem of hatchability from the standpoint of genetics. *Scientific Agriculture* 4, 1-7, 1923 c.
- DUNN, L. C., The variation of eggs in the rate at which they lose weight. Part IV. *Poultry Science* 3, 136-148, 1923-1924. 76, 77
- DUNN, L. C., Genetic factors involved in the mortality of chick embryos. Second World's Poultry Congress and Exhibition held at Barcelona, Spain, May 10-18, 1924. Book of the Congress, 2nd part, pp. 61-67, 1924. 178
- DUNN, L. C., Selective fertilization in fowls. *Poultry Science* 6, 201-214, 1927 a. 128
- DUNN, L. C., The occurrence of chondrodystrophy in chick embryos. II. The genetic evidence. *Archiv für Entwicklungsmechanik* 110, 341-365, 1927 b. 193
- DUNN, L. C., The effect of inbreeding and crossbreeding on fowls. *Verhandlungen des V. Internationalen Kongresses für Vererbungswissenschaft Berlin, 1927*, 1, 609-617, 1928. 171-174
- DUNN, L. C. and W. LANDAUER, The lethal nature of the "Creepers" variation in the domestic fowl. *American Naturalist* 60, 574-575, 1926. 138
- DUNN, L. C. and W. LANDAUER, The genetics of the rumpless fowl with evidence of a case of changing dominance. *Journal of Genetics* 29, 217-243, 1934. 184
- DUZGÜNES, O., The effect of inbreeding on reproductive fitness of S.C.W. Leghorns. *Poultry Science* 29, 227-235, 1950. 175
- EBBELL, H., Über den Einfluss von "Unden" auf die Brutergebnisse. *Archiv für Geflügelkunde* 12, 117-123, 1938. 107
- EBBELL, H., Über den Einfluss der Beleuchtung von Zuchttieren auf die Schlupfergebnisse. *Archiv für Kleintierzucht* 1, 57-63, 1940.
- EDGAR, S. A., D. S. BOND, P. MELIUS and G. R. INGRAM, The effect of a toxic substance in fat on poultry. (Abstract). *Poultry Science* 37, 1200-1201, 1958. 110
- EDMOND, H. D., Carbon dioxide under sitting hens. Report Storrs Agricultural Experiment Station 1907, pp. 157-162. 65
- EDWARDS, C. L., The physiological zero and the index of development for the egg of the domestic fowl, *Gallus domesticus*. *American Journal of Physiology* 6, 351-397, 1902. 48
- EKEBERG, C. G., Chinesernes sätt att utkläcka ägg. *Kongl. Vetenskaps Akademiens Handlingar* 29, 188-191, 1768. 13
- ELAM, J. F., L. L. GEE and J. R. COUCH, Effect of feeding penicillin on the life cycle of the chick. *Proceedings of the Society for Experimental Biology and Medicine* 77, 209-213, 1951. 101

- ELAM, J. F., R. L. JACOBS and J. R. COUCH, The effect of prolonged feeding of antibiotics upon the performance of laying hens. *Poultry Science* 32, 792-795, 1953. 101
- EL-AYADI, M. N. and H. M. EL-IBIARY, Variations in fertility and hatchability of Baladi and Leghorn eggs. *Alexandria Journal of Agricultural Research* 5, 69-88, 1957.
- ELLIS, J. B. and L. MORRIS, Factors involved in hatching chicken and turkey eggs at high elevations. *Poultry Science* 26, 635-638, 1947. 61
- ENDER, F., Über die Bedeutung des E-Vitamins für die Hühnerzucht. *Zeitschrift für Vitaminforschung* 4, 106-111, 1935. 107
- ENGEL, R. W., P. H. PHILLIPS and J. G. HALPIN, The effect of riboflavin deficiency in the hen upon embryonic development of the chick. *Poultry Science* 19, 135-142, 1940. 95
- ERANMUS, J. E., Hatchability of fertile eggs produced by reciprocal matings between the Australorp and Leghorn breeds of poultry. XI Congreso Mundial de Avicultura, Mexico, D.F., 21 to 28 September 1958. 181
- ERIKSSON, S., The influence of shell porosity on hatchability of hen's eggs and the effect of choline added to a balanced chick ration. *Kungl. Lantbrukshögskolans Annaler* 18, 21-28, 1951. 84
- ERMAN, (letter to Oken), *Isis oder Encyclopädische Zeitung von Oken* 1818, I, 122-124. 65
- ESTIENNE, C., *L'Agriculture et Maison Rustique*, Paris (Jacques du Puys), 1567. 26
- EVANS, R. J., A. C. GROSCHKE and H. A. BUTTS, Effect of vitamin B₁₂ on pantothenic acid metabolism in the chick. *Archives of Biochemistry and Biophysics* 31, 454-456, 1951. 98
- EYCLESHYMER, A. C., Some observations and experiments on the natural and artificial incubation of the egg of the common fowl. *Biological Bulletin* 12, 360-374, 1906-1907. 62
- FEDERLEY, H., Die Bedeutung der Kreuzung für die Evolution. *Jenaische Zeitschrift für Naturwissenschaft* 67, 364-386, 1932. 169
- FELDHAUS, F. M., *Die Technik der Vorzeit, der geschichtlichen Zeit und der Naturvölker*, Leipzig and Berlin, 1914. 18
- FELGÈRE, Incubation des poulets. Extrait d'une lettre adressée à M. Darcet, par le propriétaire des bains et étuves de Chaudes-Aigues (Cantal). *Journal des connaissances usuelles et pratiques* 7, 129-130, 1828. 43
- FELL, H. B. and W. LANDAUER, Experiments on skeletal growth and development in vitro in relation to the problem of avian phocomelia. *Proceedings of the Royal Society of London, B* 118, 133-154, 1935. 196
- FERDINANDOV, V. V., Vnutriialisevye temperatury pri estestvennoi inkubatsii. (Internal egg temperature in natural incubation). *Doklady Vsesoiuznoi Akademii s-kh nauk imeni V. I. Lenina, Ptitsevostvo* 1941, No. 8, 33-38.
- FÈRÈ, C., Note sur l'influence de la température sur l'incubation de l'oeuf de poule. *Journal de l'Anatomie et de la Physiologie* 30, 352-365, 1894.
- FÈRÈ, C., Réponses à quelques questions du questionnaire concernant les oeufs et l'incubation chez les oiseaux domestiques. *Ornis* 11, 425-426, 1900-1901. For further references see Strong (1939). 55
- FERGUSON, T. M., W. F. ALEXANDER and J. R. COUCH, Changes in the nervous system of the vitamin B₁₂-deficient chick embryo (Abstract). *Poultry Science* 35, 1141, 1956. 100
- FERGUSON, T. M. and J. R. COUCH, Gross and histological anomalies of B₁₂-deficient chick embryos. *Federation Proceedings* 13, 456-457, 1954 a. 100

- FERGUSON, T. M. and J. R. COUCH, Further gross observations on the B₁₂-deficient chick embryo. (Abstract: Poultry Science 33, 1054, 1954). Journal of Nutrition 54, 361-370, 1954 b. 100
- FERGUSON, T. M., R. H. RIGDON and J. R. COUCH, A pathological study of vitamin B₁₂-deficient chick embryos. Archives of Pathology 60, 393-400, 1955. 100
- FERRIS, J. F., Practical Artificial Incubation. Albany (Ferris Publishing Co.), 1880. 24, 44
- FÉRY-D'ESCLANDS, A., étude sur l'incubation artificielle. Bulletin Mensuel de la Société d'Acclimatation 3e série 2, 582-585, 1875. 39, 41
- FÉRY-D'ESCLANDS, A., étude sur l'incubation artificielle. Bulletin de la Société d'Acclimatation 3e série 4, 545-550, 1877.
- FISCHER, J., Das Problem der Brütung. Eine thermo-biologische Untersuchung. Leipzig (Quelle & Meyer), 1913. 55
- FLEAY, D. H., Nesting habits of the brush-turkey. Emu 36, 153-163, 1937. 7
- FORGET, A., L'aviculture et l'incubation artificielle. Paris (G. Delarue), 1895.
- FORTUNE, R., Three Years' Wanderings in the Northern Provinces of China, Including a Visit to the Tea, Silk, and Cotton Countries; with an Account of the Agriculture and Horticulture of the Chinese, New Plants, etc. 2nd edition. London (John Murray), 1847. 13
- FOX, S. and R. S. MARTIN, The hatchability of eggs from hens fed rations containing different protein supplements. World's Poultry Science Journal 16, 4-5, 1960.
- FRANCIS, D. W. and C. S. SHAFFNER, An investigation of the morphological changes in young chickens and the reproductive performance of adult chickens fed furazolidone or nitrofurazone. Poultry Science 35, 1371-1381, 1956. 111
- FRANCISCO, A. A., G. S. CHAN and F. M. FRONDA, Protein supplements in poultry rations: II. Comparative effects of shrimp meal, meat scraps, tankage, and fish meal as supplements in rations for laying hens. Philippine Agriculturist 22, 685-697, 1934. 108
- FRANK, N. A. and B. H. EDGINGTON, Agglutinin content of eggs from Salmonella pullorum infected hens. Poultry Science 16, 442-444, 1937. 200
- FRANKE, K. W., A. L. MOXON, W. E. POLEY and W. C. TULLY, Monstrosities produced by the injection of selenium salts into hens' eggs. Anatomical Record 65, 15-22, 1936. 113
- FRANKE, K. W. and W. C. TULLY, A new toxicant occurring naturally in certain samples of plant foodstuffs. V. Low hatchability due to deformities in chicks. Poultry Science 14, 273-279, 1935. 113
- FRANKE, K. W. and W. C. TULLY, A new toxicant occurring naturally in certain samples of plant foodstuffs. VII. Low hatchability due to deformities in chicks, produced from eggs obtained from chickens of known history. Poultry Science 15, 316-318, 1936. 113
- FRAPS, R. M., Effect of reduced atmospheric pressure on hatchability of the hen's egg. Science 101, 339, 1945. 51
- FRAPS, R. M., H. A. SOHN and M. W. OLSEN, Some effects of multiple pellet implants of diethylstilbestrol in 9 week old chickens. Poultry Science 35, 665-668, 1956. 107
- FREDERIC II of HOHENSTAUFFEN, The Art of Falconry being the De arte venandi cum avibus. Translated and edited by C. A. Wood and F. M. Fyfe. Stanford University Press, 1943 (first, and incompletely, printed at Augsburg, 1596). 21
- FRIEDMANN, H., A case of apparently adaptive acceleration of embryonic growth-rate in birds. Biological Bulletin 53, 343-345, 1927. 8

- FRIEDMANN, H., The parasitic habit in ducks, a theoretical consideration. *Proceedings of the United States National Museum* 80, Article 18, 1-7, 1932. 7
- FRITH, H. J., Incubation in the Mallee Fowl (*Leipoa ocellata*, Megapodiidae). *Acta XI Congressus Internationalis Ornithologici Basel* 1954. Basel and Stuttgart (Birkhäuser) 1955, pp. 570-574. 6
- FRITH, H. J., Incubator birds. *Scientific American* 201, August, 52-58, 1959. 5, 7
- FRÖLICH, K., Experimentelle Erzeugung von Sirenen beim Hühnchen und Bemerkungen zur sekundären Körperentwicklung. *Archiv für Entwicklungsmechanik* 134, 348-356, 1936. 196
- FRONDA, F. M., Mammoth incubators in the Philippines. *Poultry Science* 5, 67-75, 1925-1926. 15, 16
- FRONDA, F. M., Influence of earthquakes on the hatchability of incubating eggs. *Philippine Agriculture* 26, 902-906, 1938. 65
- FRONDA, F. M., Thailand: II. Animal industries. *Philippine Agriculturist* 36, 103-113, 1952. 15
- FRONDA, F. M. and J. A. BELO, Effects of sunlight on the hatching quality of eggs. *Philippine Agriculturist* 16, 477-493, 1928. 105
- FUNK, E. M., Factors influencing hatchability in the domestic fowl. *Missouri Agricultural Experiment Station Bulletin* 341, 1934 a. 48, 52, 53, 69, 72, 77, 115, 117, 118, 121, 132, 133, 174, 175
- FUNK, E. M., Relation of time of laying to hatchability. *Poultry Science* 13, 184-187, 1934 b. 121, 122, 125
- FUNK, E. M., The relation of size of clutch and position of the egg in the clutch to hatching results. *Poultry Science* 18, 350-353, 1939. 126
- FUNK, E. M. and H. V. BIELLIER, The minimum temperature for embryonic development in the domestic fowl (*Gallus domesticus*). *Poultry Science* 23, 538-540, 1944. 48
- FUNK, E. M. and J. F. FORWARD, Effect of washing soiled eggs on hatchability. *Poultry Science* 28, 155-157, 1949a.
- FUNK, E. M. and J. F. FORWARD, The relationship of egg shell color to hatchability in New Hampshires. *Poultry Science* 28, 577-580, 1949b. 81
- FUNK, E. M. and J. FORWARD, Effect of humidity and turning of eggs before incubation on hatching results. *Missouri Agricultural Experiment Station Bulletin* 554, 1951. 51, 53, 81
- FUNK, E. M. and J. F. FORWARD, Effect of multiple plane turning of eggs during incubation on hatchability. *Missouri Agricultural Experiment Station Research Bulletin* 502, 1952. 63
- FUNK, E. M. and J. FORWARD, The effect of angle of turning eggs during incubation on hatchability. *Missouri Agricultural Experiment Station Bulletin* 599, 1953. 63
- FUNK, E. M. and J. FORWARD, The relation of angle of turning and position of the egg to hatchability of chicken eggs. *Poultry Science* 39, 784-785, 1960. 63
- FUNK, E. M., J. FORWARD and H. L. KEMPSTER, Effect of holding temperatures on hatchability of eggs. *Missouri Agricultural Experiment Station Bulletin* 539, 1950. 49, 50, 51
- FUNK, E. M. and H. L. KEMPSTER, Egg weight in the domestic fowl. *Missouri Agricultural Experiment Station Bulletin* 332, 1934. 123
- FÜRER, Christophori Füreri ab Haimendorf, Equitis Aurati, Duumviri Reip. Notibergensis primarii, & in rebus bellicis Consiliarii supremi etc. *Itinerarium Aegypti, Arabiae, Palaestinae, Syriae aliarumque regionum orientalium. Norimbergae (Officina Abrahami Wagenmanni), 1621. 19*

- GABRIEL, M. L., Production of strophosomy in the chick embryo by local applications of colchicine. *Journal of Experimental Zoology* 101, 351-354, 1946. 196
- GALLERA, J., O sztucznem wytwarzaniu potworow platyneurycznych. (Production artificielle des monstres platyneuriques). *Folia morphologica* 6, 203-251, 1935-1936. 196
- GALLITZIN, D., Lettre sur quelques objets d'électricité, adressée à l'Académie Impériale des Sciences de St. Pétersbourg, par S. E. Mr. le Prince Dimitri de Gallitzin. *Acta Academiae Scientiarum Imperialis Petropolitanae pro anno MDCCLXXVII, Pars Posterior*, pp. 25-38, Petropoli 1780. 41
- GALLUP, W. D. and L. C. NORRIS, Studies on the importance of manganese in the nutrition of poultry. *Poultry Science* 16, 351-352, 1937. 111
- GALLUP, W. D. and L. C. NORRIS, The effect of a deficiency of manganese in the diet of the hen. *Poultry Science* 18, 83-88, 1939. 111
- GALLUZZI, Istoria del granducato di Toscana sotto il governo della Casa Medici 4, Firenze (R. del Vivo), 1781. 22
- GAULTIER, Rapport sur l'établissement d'incubation artificielle de M. Felgère, à Chaudes-Aigues, département du Cantal; par M. Gaultier de Claubry. *Bulletin de la Société d'encouragement pour l'industrie nationale* 30, 272-274, 1831. 43
- GAULTIER, Rapport fait par M. Gaultier de Claubry, au nom du Comité des arts chimiques, sur l'application de la chaleur des eaux thermales à l'incubation artificielle. *Bulletin de la Société d'encouragement pour l'industrie nationale* 30, 322-324, 1831. 43
- GEER, W. C., Thermostats and thermoregulators. *Journal of Physical Chemistry* 6, 85-105, 1902. 31
- GEMOLL, W., Untersuchungen über die Quellen, den Verfasser und die Abfassungszeit der Geoponica. *Berliner Studien für classische Philologie und Archaeologie* 1, 1-280, 1884. 24
- GEOFFROY-SAINT-HILAIRE, A., Les hydro-incubateurs exploités industriellement à Gambais par MM. E. Rouillier-Arnoult et E. Arnoult. *Bulletin Mensuel de la Société d'Acclimatation 3e série* 2, 713-720, 1875.
- GEOFFROY-SAINT-HILAIRE, E., Sur les déviations organiques provoquées et observées dans un établissement d'incubations artificielle. *Mémoires du Muséum d'Histoire Naturelle* 13, 289-296, 1825 (also in *Journal Complémentaire du Dictionnaire des Sciences Médicales* 24, 256-262, 1826). 64
- GEOFFROY-SAINT-HILAIRE, E., Des différens états de pesanteur des oeufs au commencement et à la fin de l'incubation. *Journal complémentaire des sciences médicales* 7, 271-278, 1830. 75
- GEOFFROY-SAINT-HILAIRE, I., Historie Générale et Particulière des Anomalies de l'Organisation chez l'Homme et les Animaux 3, Bruxelles (Société Belge de Librairie), 1837. 53
- GERICKE, A. M., Two black Australorp hens which turned white in colour. *South African Journal of Science* 31, 425-432, 1934. 167
- GERRIETS, E., Aureomycin in der Fütterung von Legehennen. *Archiv für Geflügelkunde* 24, 329-335, 1960. 101
- GERRY, R. W., C. W. CARRICK, R. E. ROBERTS and S. M. HAUGE, Raw rock phosphate in laying rations. *Poultry Science* 28, 19-23, 1949.
- GESNER, Contr. Gesneri Tigvrini, Medicinae et Philosophiae Professoris in Schola Tigurina. *Historiae Animalium Liber III. Qui est de Avium natura*. Francoforti (In Bibliopolia Andreae Cambieri), 1601. 19
- GEYELIN, G. K., Poultry Breeding in a Commercial Point of View, as carried out by the National Poultry Company (Limited), Bromley, Kent. 6th edition. New York, 1881 (first edition 1867). 43

- GIACOMINI, C., Influenza dell'arie rarefatta sullo sviluppo dell'ovo di pollo. *Giornale della R. Accademia di Medicina di Torino* 42, 561-576, 1894. 61
- GILBERT, A. G., Report of the poultry manager. *Experimental Farms Reports for 1891. Appendix to the Report of the Minister of Agriculture, Ottawa, 1895*, pp. 227-251. 81
- GILBERT, A. G., Report of the poultry manager. *Canadian Experimental Farm Report for 1904*, pp. 283-311. 128
- GILBERT, A. G., Report of the poultry manager. *Canadian Experimental Farm Report for 1905*, pp. 233-261. 128
- GILFILLAN, S. C., *The Sociology of Invention*. Chicago (Follet Publishing Company), 1935. 46
- GILLIS, M. B., G. F. HEUSER and L. C. NORRIS, Quantitative requirements of the hen for pantothenic acid. *Abstract. Poultry Science* 21, 470, 1942a. 97
- GILLIS, M. B., G. F. HEUSER and L. C. NORRIS, The need for pantothenic acid and an unidentified factor in reproduction in the domestic fowl. *Journal of Nutrition* 23, 153-163, 1942b. 97
- GILLIS, M. B., G. F. HEUSER and L. C. NORRIS, The pantothenic acid requirement of hens for reproduction. *Abstract. Poultry Science* 26, 540, 1947. 97
- GILLIS, M. B., G. F. HEUSER and L. C. NORRIS, Pantothenic acid in the nutrition of the hen. *Journal of Nutrition* 35, 351-363, 1948. 97
- GIOVIO, *Istorie del suo tempo di Mons. Paolo Giovio da Como, Vescovo di Nocera*, tradotta per M. Lodovico Domenichi. Venetia, 1560 (Latin edition: Florentiae, 1550-1552). 19
- de la GIRONIÈRE, P., *Twenty Years in the Philippines*. New York (Harper and Brothers), 1854. 15
- de la GIRONIÈRE, *Notice sur l'agriculture des Philippines. Élève des canards. Annales de l'agriculture des colonies et des régions tropicales* 1, 205-208, 1860. 15
- GOBIN, A., *Traité des oiseaux de basse cour, d'agrément et de produit*. 3e édition. Paris (Librarie Audot), no date. 43, 46
- GODFREY, A. B., The effect of egg weight, quantity of total albumen per egg, and quantity of thick albumen per egg on hatchability. *Poultry Science* 15, 294-297, 1936. 71, 88-90
- GODFREY, A. B. and M. OLSEN, Individual hen and breed difference in egg weight losses during incubation. *Poultry Science* 16, 216-218, 1937. 81
- GODFREY, G. F., The relationship of egg shell color to hatchability in some brown egg laying breeds. *Poultry Science* 26, 381-388, 1947. 81
- GODFREY, G. F., Shell color as a measure of shell quality. *Poultry Science* 28, 150-151, 1949a. 81
- GODFREY, G. F., The comparative efficiency of specific gravity, 14-day incubation weight-loss and egg shell color in selecting for hatchability and egg shell quality. (Abstract) *Poultry Science* 28, 764, 1949b.
- GODFREY, G. F., The effect of feeding thyroprotein on egg shell quality and hatchability. (Abstract). *Poultry Science* 28, 867-873, 1949c.
- GODFREY, G. F., Shell color as a measure of egg shell quality. *Poultry Science* 28, 150-151, 1949d. 82
- GODFREY, G. F. and R. G. JAAP, The relationship of specific gravity, 14-day incubation weight-loss and egg shell color to hatchability and egg shell quality. *Poultry Science* 28, 874-889, 1949.
- GODFREY, G. F., C. WILLIAMS and R. B. THOMPSON, The effect of egg size and rapidity of hatching on growth and reproductive performance. *Oklahoma Agricultural Experiment Station Manuscript Report Abstract No. MRA-7*, 1952. 171

- GOHORY, J., *Instrvction syr lherbe petum ditte en France lherbe de la Royné ou Medicee*, Paris, 1572. 21
- GOLDING, W. V., P. J. SCHABBLE and J. A. DAVIDSON, A breed difference in the manganese requirement of laying hens. *Poultry Science* 19, 263-269, 1940. 112
- GOLOVKOV, V. G., *Izuchenie nekotorykh khoziaistvenno-poleznykh kachestv kur iurlovskikh golosistykh nonuliatykh pitseovkhozov im I maia i rod-ailand*. (The study of some economically useful qualities of Voviferous Orloff of the Breeding Farm May 1st and of Rhode Island Red). In: *Iurlovskie kury i kholmogorskie gysi* (Orloff fowl and Kholmogor geese), edited by E. E. Penionzhkevich. *Nar-komzem R.S.F.S.R. Nauchno-issledovatel'skii institut pitsevodstva* 1939, pp. 43-53. 189
- GONZALEZ de MENDOZA, JOAN, *Historia de las cosas mas notables, ritos y costumbres del gran reyno de la China, sabidas assi por los libras de los mesmos chinas, como por relacion de religiosos y otras personas que en estado en el dicho reyno. Hecha y ordenada por el myv R. P. Maestro Fr. Joan Gonzalez de Mendoza de la orden de S. Augustin, y penitenciario apostolico a quien la Magestad Catholica embrio con su real carta y otras cosas para el Rey de aquel reyno el año 1580. En Roma, a costa de Bartholome Grassi, 1585, en la Stampa de Vincentio Accolti*. 10, 21, 23
- GONZALEZ de MENDOZA, JUAN, *The historie of the great and mightie Kingdome of China, and the situation thereof: together with the great riches, huge cities, politike government, and rare inuentions in the same. Tr. out of Spanish by R. Parke. London (E. White), 1588 (Reprinted by Hakluyt Society, 1853)*. 10, 21, 23
- GOODMAN, B. L. and G. F. GODFREY, Genetic, phenotypic and environmental correlations between some egg quality traits and egg production and hatchability (Abstract). *Poultry Science* 34, 1197, 1955.
- GOODWIN, K., W. F. LAMOREUX and G. E. DICKERSON, Maternal effects in chickens as influenced by age of dam (Abstract). *Poultry Science* 39, 1253, 1960. 115
- GOODWIN, T., L. BARTON and E. L. STEPHENSON, The effect of zoaline on chick growth and hatchability. (Abstract). *Poultry Science* 38, 1209, 1959.
- GORDON, R. F., L. G. CHUBB and C. G. STACEY, Vitamin B₁₂ and penicillin supplements in poultry nutrition. *Veterinary Record* 66, 71-74, 1954. 101
- GOTO, E. and A. W. NORDSKOG, Heterosis in poultry. 4. Estimation of combining ability variance from diallel crosses of inbred lines in the fowl. *Poultry Science* 38, 1381-1388, 1959. 175
- GOWE, R. S., Techniques for identifying fertile hens' eggs. *Poultry Science* 29, 409-413, 1950. 9
- GOWE, R. S. and J. R. HOWES, The effect of the addition of L-thyroxine to fowl semen. *Poultry Science* 35, 983-990, 1956. 130
- GOWE, R. S., A. S. JOHNSON, J. H. DOWNS, R. GIBSON, W. F. MOUNTAIN, J. H. STRAIN and B. F. TINNEY, Environment and poultry breeding problems. 4. The value of a random-bred control strain in a selection study. *Poultry Science* 38, 443-462, 1959. 176
- GOWELL, G. M., *Poultry experiments in 1900 and 1901. Maine Agricultural Experiment Station Bulletin* 79, 1902. 53
- GRABOWSKI, C. T. and J. A. PAAR, The teratogenic effects of graded doses of hypoxia on the chick embryo. *American Journal of Anatomy* 103, 313-344, 1958. 67
- GRAHAM, R. and V. M. MICHAEL, Studies on incubator hygiene. V. A. note on the hatchability of eggs inoculated with *Salmonella*, *Pasteurella*, *Staphylococci* and *Streptococci*. *Poultry Science* 15, 83-87, 1936.
- GRAHAM, W. R., *Experiments in hatching and rearing chickens. Ontario Agricultural College Bulletin* 163, 1-28, 1908. 5

- GRAHAM, W. R., Nutrition and hatchability. Report of Proceedings of the 4th World's Poultry Congress at the Crystal Palace, London, England: July 22-30, 1930, 207-210, 1931.
- GRAHAM, W. R., W. H. DAY, C. C. THOM, R. HARCOURT and H. L. FULMER, Incubation of chickens. Ontario Agricultural College Bulletin 163, 1908. 65
- GRAHAM, W. R., J. B. SMITH and W. D. McFARLANE, Results of a three year study of certain poultry rations as they affect the hatching power of hen eggs as well as the number of eggs laid. Ontario Agricultural College Bulletin 362, 1931. 103
- GRAU, C. R. and P. A. ZWEIGART, Studies of purified diets for egg production and hatchability (Abstract). Poultry Science 31, 919, 1952.
- GRAVES, J., The manner of hatching chickens at Cairo. Philosophical Transactions 10, 923-925, 1675. 19
- GRAY, P. and H. WORTHING, Experiments on chemical interference with the early morphogenesis of the chick. I. The effects of tetanus toxin on the morphogenesis of the central nervous system. Journal of Experimental Zoology 86, 423-437, 1941. 196
- di GRAZIA, A., Culture in vitro di tessuti embrionali di pollo teratologico. Rivista Patologia Sperimentale N.S. 7, 236-241, 1937. 190
- GREDINA, T. V., Vyvodnost' u bystro i medlenno operaiuchikhsia rod - ailandov (Hatchability in rapid and slow-feathering Rhode Islands). Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936, pp. 114-118. 163, 164
- GREENWOOD, A. W., The value of progeny in relation to age of dam. Harper-Adams Utility Poultry Journal 17, 478-480, 1932. 115
- GREGOROVIVS, F., The Emperor Hadrian. Translated by M. E. Robinson. London (Macmillan and Co.), 1898. 24
- GREW, N., Musaeum Royalis Societatis or a Catalogue & Description of the Natural and Artificial Rarities Belonging to the Royal Society and preserved at Gresham College. London (W. Rawlins), 1681. 35
- GRIMMELSHAUSEN, Continuatio des abendtheuerlichen Simplicissimi oder der Schluss desselben. Durch German Schleifheim von Sulstort. Mompelgart (Johann Fillion) 1669. 19
- GRODZINSKI, Z., Über die Entwicklung von unterkühlten Hühnereiern. Archiv für Entwicklungsmechanik 129, 502-521, 1933. 56
- GRODZINSKI, Z., Weitere Untersuchungen über den Einfluss der Unterkühlung auf die Entwicklung der Hühnereier. Archiv für Entwicklungsmechanik 131, 653-671, 1934. 56
- GROEBBELS, F., Der Vogel, vol. 2. Berlin (Gebrüder Borntraeger) 1937. 5, 7, 55
- GROEBBELS, F. und F. MÖBERT, Über die Lebensdauer von Vogelembryonen und die Lebensdauer des Kuckucks im Ei. Ornithologische Monatsberichte 38, 89-90, 1930. 8
- GROSCHKE, A. C. and H. R. BIRD, Value of a fermentation by-product in poultry feeds. Maryland Agricultural Experiment Station Bulletin A-6, 1941.
- GROSCHKE, A. C., M. RUBIN and H. R. BIRD, Seasonal variation in hatchability and its relation to an unidentified dietary factor. Poultry Science (Abstract 26, 541, 1947) 27, 302-307, 1948.
- GROSIER, ABBÉ, Description Générale de la Chine. Nouvelle édition. Paris (Moutard), 1787 (first edition 1785). 13, 23
- GROSSOWICZ, N., Influence of thiourea on development of the chick embryo. Proceedings of the Society for Experimental Biology and Medicine 63, 151-152, 1946. 112

- GRUENWALD, P., Studies on developmental pathology. I. The morphogenesis of a hereditary type of microphthalmia in chick embryos. *Anatomical Record* 88, 67-76, 1944. 167
- GRUENWALD, P., Malformations caused by necrosis in the embryo illustrated by the effect of selenium compounds on chick embryos. *American Journal of Pathology* 34, 77-103, 1958. 114
- GUDKIN, A. F., D. N. MURUSIDZE and T. A. SMIRNOV, Primenenie ultravioletovykh lučei pri inkubacii jaic (The use of ultraviolet rays in incubating eggs). *Pticevodstvo* 9, No. 2, 19-20, 1959. Quoted from: *Animal Breeding Abstracts* 27, 351, 1959. 106
- GUTTERIDGE, H. S., Some causes of deterioration in egg quality during shipment. *Poultry Science* 10, 402, 1930-1931. 53, 54
- HADLEY, P. B. and D. W. CALDWELL, The bacterial infection of fresh eggs. *Rhode Island Agricultural Experiment Station Bulletin* 164, 1916. 202
- HALBERSLEBEN, D. L. and F. E. MUSSEHL, Relation of egg weight to chick weight at hatching. *Poultry Science* 1, 143-144, 1921-1922. 68
- HALL, G. O. and A. L. ROMANOFF, Effect of sealing of the shell and holding temperature on hatchability of hens' eggs. *Poultry Science* 22, 354-356, 1943.
- HALL, G. O. and A. VAN WAGENEN, The association of certain measures of interior egg quality with hatchability. *Poultry Science* 15, (Abstract p. 414), 501-506, 1936. 90
- HALLER, A. VON, *Elementa physiologiae corporis humani. Editio secunda.* Lausannae (Societas Typographica) 8, 159-160, 1778. 19
- HALPIN, J. G. and C. E. HOLMES, Produce good eggs for hatching. *Wisconsin Agricultural Experiment Station Bulletin* 433, 1936.
- HALSTED, A. M., *Artificial Incubation and Incubators.* 2nd edition. New York, 1883. 46
- HAMILTON, A., Report on "Manufactures." In: *The Works of Alexander Hamilton.* Constitutional edition. New York and London (G. P. Putnam's Sons), vol. 4, 1885. 47
- HAMMERL, H., Zusammenstellung der bisher construierten Thermostaten. *Repertorium für Experimental-Physik, für physikalische Technik, mathematische und astronomische Instrumentenkunde* 18, 309-332, 385-414, 441-445; 1882. 31
- HAMMOND, J. C., The comparison of corn, milo, and hegari in the diet of laying hens. *Poultry Science* 21, 410-415, 1942. 108
- HANNAS, R. R., Embryo mortality. *Journal of the American Association of Instructors and Investigators in Poultry Husbandry* 6, 77-79, 1919-1920. 63
- HANSBOROUGH, L. A., The effect of increased nicotinic acid in the egg on the development of the chick embryo. *Growth* 11, 177-184, 1947. 98
- HARFF, Die Pilgerfahrt des Ritters Arnold von Harff von Cöln durch Italien, Syrien, Aegypten, Arabien, Aethiopien, Nubien, Palästina, die Türkei, Frankreich und Spanien, wie er sie in den Jahren 1496 bis 1499 vollendet, beschrieben und durch Zeichnungen erläutert hat. Herausgegeben von E. von Groote. Cöln (J. M. Heberle), 1860. 19
- HARMAN, M. T., Heat as a factor in producing abnormalities during incubation in the chick. *Transactions of the Kansas Academy of Science* 31, 66-76, 1928. 55
- HARRISON, J. R. and I. KLEIN, Effect of lowered incubation temperature on the growth and differentiation of the chick embryo. *Biological Bulletin* 106, 48-59, 1954. 57
- HARRY, E. G., The effect on embryonic and chick mortality of yolk contamination with bacteria from the hen. *Veterinary Record* 69, 1433-1439, 1957. 202

- HARRY, E. G., Sources of extragenital bacterial contamination of the shell, and the possible relationship between such contamination and the development of undesirable changes in egg composition. XI Congreso Mundial de Avicultura, Mexico, D.F., 21 to 28 September, 1958. 202
- HART, C. P. and H. O. STUART, The effect of certain feed supplements on the hatchability, economy, and efficiency of poultry feeding. I. Condensed buttermilk; and a mixture of cereal grasses and condensed milk. Rhode Island Agricultural Experiment Station Bulletin 289, 1943.
- HART, C. P. and H. O. STUART, The effect of different intake levels of alfalfa leaf meal in enhancing hatchability. Rhode Island Agricultural Experiment Station Miscellaneous Publication 20, 1944. 93
- HART, E. B., H. STEENBOCK, S. LEPKOVSKY, S. W. F. KLETZIEN, J. C. HALPIN and O. N. JOHNSON, The nutritional requirement of the chicken. V. The influence of ultra-violet light on the production, hatchability and fertility of the egg. *Journal of Biological Chemistry* 65, 579-595, 1925. 103, 105
- HAVERMANN, H. and R. M. WEGNER, Antibiotica in der Fütterung von Leghennen. *Archiv für Geflügelkunde* 22, 217-239, 1958. 101
- HAYS, F. A., The relation of the male to the hatchability of hens' eggs. *Science* 64, 408, 1926. 166, 183
- HAYS, F. A., Relation of age of parents to hatchability, livability and fecundity in the domestic fowl. *Poultry Science* 7, 106-115, 1927-1928. 116
- HAYS, F. A., Time interval between eggs of Rhode Island Red pullets. *Journal of Agricultural Research* 52, 633-638, 1936. 126
- HAYS, F. A., Hatchability as related to seasons and hour of laying. *Poultry Science* (Abstract 15, 414, 1936) 16, 85-89, 1937. 122
- HAYS, F. A., Time interval between clutches in Rhode Island Red Pullets. *Journal of Agricultural Research* 57, 575-581, 1938. 126
- HAYS, F. A., The importance of length of incubation period in Rhode Island Reds. *Massachusetts Agricultural Experiment Station Bulletin* 384, 1941. 136, 171
- HAYS, F. A., Egg production versus reproduction in Rhode Island Reds. *Poultry Science* 22, 118-122, 1943. 119
- HAYS, F. A., Chondrodystrophy in Rhode Island Reds. *American Naturalist* 78, 54-58, 1944. 152
- HAYS, F. A., The primary sex ratio in domestic chickens. *American Naturalist* 79, 184-186, 1945. 170, 171
- HAYS, F. A., Sex influence on embryonic death rate in chicks. *Science* 110, 553, 1949. 170
- HAYS, F. A., Temperature and relative humidity in the incubation room and embryonic mortality. *Poultry Science* 30, 151-152, 1951a. 202
- HAYS, F. A., Fertility and hatchability in Rhode Island Reds. *Poultry Science* 30, 153, 1951b. 127
- HAYS, F. A., Possible effects of sex-linked genes on reproduction and fecundity in Rhode Island Reds. *Poultry Science* 31, 826-829, 1952a.
- HAYS, F. A., Sex ratio in Rhode Island Red chicks at hatching. *Poultry Science* 31, 1094, 1952b. 170
- HAYS, F. A., Factors affecting sex ratio at eight weeks in Rhode Island Reds. *Poultry Science* 33, 230-233, 1954. 170
- HAYS, F. A., Breeding for high egg production. *Massachusetts Agricultural Experiment Station Bulletin* 504, no date (1959). 183
- HAYS, F. A. and C. NICOLAIDES, Variability in development of fresh-laid hen eggs. *Poultry Science* 13, 74-90, 1934. 184

- HAYS, F. A. and R. SANBORN, The inheritance of fertility and hatchability in poultry. Massachusetts Agricultural Experiment Station Technical Bulletin 6, 1924. 114, 127, 179, 181, 182
- HAYS, F. A. and E. W. SPEAR, Embryonic death rate and sex ratio in chicks. *Science* 112, 792, 1950. 170
- HAYS, F. A. and E. W. SPEAR, Losses in egg weight during incubation associated with hatchability. *Poultry Science* 30, 106-107, 1951. 81
- HAYS, F. A. and A. H. SUMBARDO, Physical characters of eggs in relation to hatchability. *Poultry Science* 6, 196-200, 1926-1927. 68, 74, 77
- HAYS, F. A. and D. W. TALMADGE, Hatchability in Rhode Island Reds as affected by age of parents. *Journal of Agricultural Research* 78, 285-290, 1949. 116, 119
- HAZEL, L. N. and W. F. LAMOREUX, Family sex ratios in the fowl. *Journal of Heredity* 27, 333-334, 1946. 171
- HÉBERT, J. et H. LAUGIER, Probabilité d'éclosion des oeufs en fonction de leur poids. *Revue Canadienne de Biologie* 2, 113-119, 1943. 71
- HEIMAN, V., The relative vitamin G content of dried whey and dried skim milk. *Poultry Science* 14, 137-146, 1935. 94
- HENDERSON, E. W., Growth and development with special reference to domestic animals. XVI. The influence of temperature and breeding upon the rate of growth of chick embryos. *Missouri Agricultural Experiment Station Research Bulletin* 149, 1930.
- HENDERSON, E. W., Influence of temperature on length of artificial incubation period of *Gallus domesticus*. *Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939*, pp. 180-184. 188
- HENDERSON, E. W., Hatching ability of poultry. I. Texture of egg shells in relation to loss of weight during incubation. *The Quarterly Bulletin, Michigan Agricultural Experiment Station* 24, 118-122, 1941. 84
- HENDERSON, E. W., Hatching ability of poultry. II. Texture of egg shells in relation to hatching power. *The Quarterly Bulletin, Michigan Agricultural Experiment Station* 25, 41-47, 1942a. 84
- HENDERSON, E. W., Hatching ability of poultry. III. The market quality criterion—Mobility of yolk and hatchability. *The Quarterly Bulletin, Michigan Agricultural Experiment Station* 25, 151-156, 1942b. 94
- HENDERSON, E. W., Hatchability of purebred and crossbred chick embryos. *Quarterly Bulletin of the Michigan Agricultural Experiment Station* 34, 83-88, 1951a. 179
- HENDERSON, E. W., Inheritance of hatching power in nine generations of Dark Cornish. *Quarterly Bulletin of the Michigan Agricultural Experiment Station* 34, 166-171, 1951b. 179
- HENDERSON, E. W., Which chicks hatch first - male or female? *Quarterly Bulletin of the Michigan Agricultural Experiment Station* 38, 362-364, 1956. 171
- HENDERSON, E. W., Hatching power of purebred vs. crossbred chick embryos. *Quarterly Bulletin of the Michigan Agricultural Experiment Station* 39, 570-577, 1957. 179
- HENDERSON, E. W., The influence of inheritance on hatching power of 18 generations of chickens. *Quarterly Bulletin of the Michigan Agricultural Experiment Station* 42, 596-606, 1960. 175
- HENDERSON, E. W., Fertility percentage of hens not a good index of hatching power. *Quarterly Bulletin Michigan Agricultural Experiment Station* 42, 913, 1960.
- HERPIN, Rapport fait par M. Herpin, au nom du comité des arts économiques, sur un appareil d'incubation artificielle établi par feu Bonnemain et perfectionné par M. Sorel. *Bulletin de la Société d'encouragement pour l'industrie nationale* 39, 252-256, 1840. 43

- HESEN, B., The social and economic roots of Newton's "Principia." In: Science at the Cross Roads. London (Kniga Ltd.), 1931. 46
- HEUSER, F. G., Nutritional factors affecting hatchability of eggs. Report of Proceedings of the World's Poultry Congress, Ottawa, Canada, July 27 to August 4, 1927, pp. 207-214. 104
- HEUSER, G. F., Protein in poultry nutrition—a review. Poultry Science 20, 362-368, 1941. 108
- HEUSER, G. F., Feeding Poultry. Chapter 14, Feeding and Management of Breeders. 2. edition, New York (John Wiley & Sons), 1955. 92
- HEUSER, G. F. and L. C. NORRIS, Soybean oil meal in hen rations. Poultry Science 23, 371-376, 1944. 109
- HEUSER, G. F., L. C. NORRIS, H. L. LUCAS and G. F. COMBS, Further studies on the need by poultry for an unidentified factor associated with animal proteins. Abstract. Poultry Science 25, 403, 1946.
- HEYN, G., Beobachtungen über die Wirkung von T-Vitamin (Goetsch) bei Hühnern. Zeitschrift für Vitamin-, Hormon- und Fermentforschung 4, 121-136, 1951. 107
- HEYWANG, B. W., Hatchability in relation to the fat content of the diet. Poultry Science 21, 521-524, 1942. 109
- HEYWANG, B. W., The effect of D-activated animal sterol and sunlight on hatchability. Poultry Science 23, 165-169, 1944a. 105
- HEYWANG, B. W., The hatchability of eggs from hens receiving cod-liver oil and direct sunlight. Poultry Science 23, 230-233, 1944b.
- HEYWANG, B. W., Fertility and hatchability when the environmental temperature of chickens is high. Poultry Science 23, 334-339, 1944c. 50
- HEYWANG, B. W., Gathering and storing hatching eggs during hot weather. Poultry Science 24, 434-437, 1945. 51
- HEYWANG, B. W., The level of vitamin A in the diet of laying and breeding chickens during hot weather. Poultry Science 31, 294-301, 1952.
- HEYWANG, B. W., The effect of high levels of an antibiotic on laying chickens during hot weather. Poultry Science 35, 1196-1200, 1956. 101
- HEYWANG, B. W., The effect of arsanilic acid and low levels of antibiotics on laying chickens during hot weather. Poultry Science 38, 854-858, 1959. 101
- HEYWANG, B. W. and H. R. BIRD, Supplements for cottonseed meal in diets for chickens. Poultry Science 29, 486-495, 1950. 109
- HEYWANG, B. W. and H. R. BIRD, Failure of several amino compounds and of cardine meal to inactivate gossypol in diets of breeding chickens. Poultry Science 31, 805-809, 1952.
- HEYWANG, B. W., H. R. BIRD and A. M. ALTSCHUL, The effect of pure gossypol on hatchability and egg weight. Poultry Science 29 (Abstract p. 763), 916-920, 1950. 109
- HEYWANG, B. W., H. R. BIRD and R. P. KUPPERMAN, The loss or inactivation of pure gossypol in a mixed diet. Poultry Science 31, 35-39, 1952. 109
- HEYWANG, B. W., C. A. DENTON and H. R. BIRD, The effect of the dietary level of cottonseed meal on hatchability. Poultry Science 28, 610-617, 1949. 109
- HILL, D. C., J. D. McCONACHIE, K. M. GARTLEY and H. D. BRANION, The use of a commercial animal protein factor supplement in a hatching ration. Poultry Science 29, 744-745, 1950. 100
- HILL, F. W., L. C. NORRIS and M. L. SCOTT, The riboflavin requirement of single comb White Leghorns for reproduction (Abstract). Poultry Science 33, 1059, 1954. 95

- HILL, J. F., G. E. DICKERSON and H. L. KEMPSTER, Some relationships between hatchability, egg production and adult mortality. (Abstract). *Poultry Science* 33, 1059-1060, 1954. 183
- HINRICHS, M. A., Modifications of development on the basis of differential susceptibility to radiation. IV. Chick embryos and ultra-violet radiation. *Journal of Experimental Zoology* 47, 309-342, 1927. 196
- HOESCH, W. and G. NIETHAMMER, Die Vogelwelt Deutsch-Südwestafrikas, namentlich des Damara- und Nomalandes. *Journal für Ornithologie* 88, Sonderheft 1-404, 1940. 8
- HOGAN, A. G., L. R. RICHARDSON, H. PATRICK and H. L. KEMPSTER, Perosis due to a vitamin deficiency. *Journal of Nutrition* 21, 327-340, 1941. 110
- HOLMES, A. D., H. E. BROWN, J. W. SMITH, G. B. TREADWELL and W. M. E. WHITELOCK, Studies of the vitamin potency of cod liver oils. XIX. Influence of cod liver oil on reproduction. *Poultry Science* 5, 110-116, 1925-1926. 103
- HOLMES, A. D., A. W. DOOLITTLE and W. B. MOORE, Studies on the vitamin potency of cod liver oils. XXI. The stimulation of reproduction by fat-soluble vitamins. *Journal of the American Pharmaceutical Association* 16, 518-527, 1927. 92
- HOLMES, C. E., J. G. HALPIN and C. A. HERRICK, Rickets in laying pullets fed sulphur. *Poultry Science* 20, 46-50, 1941. 194
- HOOKE, R., *Lampas: or, Description of some Mechanical Improvements of Lamps & Waterpoises. Together with some other Physical and Mechanical Discoveries.* London (John Martyn), 1667. Reprinted in R. T. Gunther, *Early Science in Oxford*, vol. 8, *The Cutler Lectures of Robert Hooke.* Oxford, 1931. 32-36
- HOOKE, R., *The Diary of Robert Hooke M.A. M.D. F.R.S. 1672-1680.* Edited by H. W. Robinson and W. Adams. London (Taylor and Francis), 1935. 32
- HORLACHER, W. R., R. M. SMITH and W. H. WILEY, Crossbreeding for broiler production. *Arkansas Agricultural Experiment Station Bulletin* 411, 1941. 178
- HUGHES, J. S., L. F. PAYNE and W. L. LATSHAW, The influence of ultraviolet light on leg weakness in growing chicks and on egg production. *Poultry Science* 4, 151-156, 1924-1925. 103
- HUNSAKER, W. G. and J. R. AITKEN, The effect of "visible" light on the fertilizing capacity of fowl spermatozoa. *Poultry Science* 39, 865-867, 1960.
- HUNT, C. H., A. R. WINTER and R. M. BETHKE, Further studies on the riboflavin requirements of the chicken. *Poultry Science* 18, 330-336, 1939. 95
- HUNTER, A., *Georgical Essays* 4, 306-315, Essay XI. On hatching chickens. York 1803.
- HUSTON, T. M. and J. L. CARMON, The influence of high environmental temperature on fertility and hatchability of eggs of domestic fowl. *Physiological Zoology* 31, 232-235, 1958. 51
- HUSTON, T. M., J. R. PALMER and J. L. COMMON, The effects of washing on the hatchability of hen eggs. *Poultry Science* 36, 557-562, 1957.
- HUTT, F. B., Studies in embryonic mortality in the fowl. I. The frequencies of various malpositions of the chick embryo and their significance. *Proceedings of the Royal Society of Edinburgh* 49, 118-130, 1929. 190
- HUTT, F. B., The genetics of the fowl. I. The inheritance of frizzled plumage. *Journal of Genetics* 22, 109-127, 1930. 131
- HUTT, F. B., On the origin, common types and economical significance of teratological monsters in embryos of the domestic fowl. Report of Proceedings of the 4th World's Poultry Congress at the Crystal Palace, London, England: July 22-30, 1930, 195-202, 1931.
- HUTT, F. B., Embryonic mortality in the fowl. VII. On the relation of malpositions to the size and shape of eggs. *Poultry Science* 17, 345-352, 1938. 192

- HUTT, F. B., A relation between breed characteristics and poor reproduction in White Wyandotte fowls. *American Naturalist* 74, 148-156, 1940. 138
- HUTT, F. B., Semi-lethal action of the gene for extension of black pigment in the fowl. *Records of the Genetics Society of America* No. 18, 95-96, 1949. 163
- HUTT, F. B., Lethal action of the gene for extension of black pigment in the fowl. *Genetics* 36, 213-234, 1951. 163, 170
- HUTT, F. B. and J. R. CAVERS, The lethal nature of certain malpositions of the chick embryo. *Poultry Science* 10, 403-404, 1930-1931.
- HUTT, F. B. and R. K. COLE, Heterosis in an inter-strain cross of White Leghorns. *Poultry Science* 31, 365-374, 1952. 175
- HUTT, F. B. and R. K. COLE, Resistance to lymphomatosis in the fowl in relation to reproduction. *Nature* 176, 1178-1179, 1955. 203
- HUTT, F. B. and A. W. GREENWOOD, Studies in embryonic mortality in the fowl. II. Chondrodystrophy in the chick. *Proceedings of the Royal Society of Edinburgh* 49, 131-144, 1928-1929a. 193
- HUTT, F. B. and A. W. GREENWOOD, Studies in embryonic mortality in the fowl. III. Chick monsters in relation to embryonic mortality. *Proceedings of the Royal Society of Edinburgh* 49, 145-154, 1928-1929b.
- HUTT, F. B. and A. M. PILKEY, Studies in embryonic mortality in the fowl. IV. Comparative mortality rates in eggs laid at different periods of the day and their bearing on theories of the origin of monsters. *Poultry Science* 9, 194-203, 1929-1930. 119-122
- HUTT, F. B. and A. M. PILKEY, Studies in embryonic mortality in the fowl. V. Relationship between positions of the eggs and frequencies of malpositions. *Poultry Science* 13, 3-13, 1934. 191
- HUTT, F. B. and P. D. STURKIE, Genetics of the fowl. IX. Naked. A new sex-linked mutation. *Journal of Heredity* 29, 371-379, 1938. 166
- HYMAN, L. H., The metabolic gradients of vertebrate embryos. III. The chick. *Biological Bulletin* 52, 1-39, 1927. 196
- HYRE, H. M. and G. O. HALL, The constancy of hatching power in hens. *Poultry Science* 11, 166-171, 1932. 115, 127
- IGUCHI, K. and K. MITAMURA, Fukachu no keiran ni oyobosu shigai kosen no Eikyo ni tsukide (The influence of ultraviolet rays upon the hatching of hen's eggs 1st report). *Journal of the Society of Agriculture and Forestry Sapporo, Japan* 19, 420-428, 1928. 105
- INGRAM, C., The incubation period in the cuckoo. *British Birds* 1, 291-292, 1907-1908. 8
- INGRAM, G. R., W. W. CRAVENS, C. A. ELVEHJEM and J. C. HALPIN, Relation of tryptophan and lysine to egg production, hatchability and composition of the protein of hens' eggs. *Poultry Science* 29, 793-803, 1950. 108
- INMAN, O. R., Developmental anomalies in the talpid lethal(tata) chick. Ph.D. thesis, Cornell University, 1946. 144
- INSKO, JR., W. M., The effects of cod liver oil on embryo mortality. *Poultry Science* 13, 306, 1934. 192
- INSKO, JR., W. M., S. J. LOWRY and L. M. CALDWELL, The all-pullet flock vs. the hen flock. *Kentucky Agricultural Experiment Station Bulletin* 560, 1951. 115
- INSKO, JR., W. M. and M. LYONS, The effect of cod liver oil in the diet of the mother hen on embryo mortality and on the calcium and phosphorus content of the embryo. *Kentucky Agricultural Experiment Station Bulletin* 363, 1936. 103, 104
- INSKO, JR., W. M. and J. M. MARTIN, Effect of frequent turning on hatchability and distribution of embryo mortality. *Poultry Science* 12, 282-286, 1933. 63, 192

- INSKO, JR., W. M., D. G. STEELE and E. T. WIGHTMAN, Reproductive phenomena in aging hens. Kentucky Agricultural Experiment Station Bulletin 498, 1947. 116
- IVANOV, V. G., Razlichnala chuvstivitel'nost' samtsov i samok embrionov kur (Difference in sensitivity of male and female chicken embryos). Doklady Akademii Nauk SSSR 100, 829-832, 1955a. 171
- IVANOV, V. G., Vliianie sroka khraneniia iaits na sootnoshenie polov v potomstve kur (The effect of the egg storage period on the sex ratio in chick offspring). Doklady Akademii Nauk SSSR 100, 1021-1023, 1955b. 171
- JACKSON, H. W., Poultry experiments. Experiments in incubation. Pennsylvania State College Agricultural Experiment Station Bulletin 120, 3-15, 1912. 50, 53
- JACOBS, R. L., J. F. FLAM, J. H. QUISENBERRY and J. R. COUCH, Dehydrated alfalfa leaf meal as a source of vitamins and unidentified factors for the mature fowl. Poultry Science 32, 812-813, 1953. 101
- JAEGER, F. M., Cornelis Drebbel en zijne tijdgenooten. Groningen (P. Noordhoff). 1922.
- JARDEL, E., Note sur une couveuse artificielle. Système Annamite. Bulletin de la Société Nationale d'Acclimatation de France 63, 315-321, 1916. 15
- JEAN-BLAIN and R. BARONE, Les phases critiques embryologiques et anatomiques de l'incubation. Annales de la Nutrition et de l'Alimentation 8, 173-192, 1954.
- JEFFREY, F. P., Hereditary microphthalmia in the domestic fowl. Journal of Heredity, 32, 310-312, 1941. 167
- JEFFREY, F. P., Methods of breeding chickens for high egg production. I. Applying the progeny test to a small flock. New Jersey Agricultural Experiment Station Bulletin 714, 1944. 175
- JEFFREY, F. P. and C. S. PLATT, A 3-year study of out-of-season hatching. New Jersey Agricultural Experiment Station Bulletin 687, 1941.
- JENSEN, L. S. and J. MCGINNIS, Effect of different diets and unidentified factor supplements on reproduction in chickens and early chick growth. Poultry Science 36, 312-319, 1957. 101
- JOHNSON, E. A., A. M. PILKEY and A. W. EDSON, Effect of supplementary iodine on reproduction in the fowl. Poultry Science 14, 16-23, 1935. 112
- JOHNSON, E. L., Vitamin B₁₂ requirements of hens as affected by choline and penicillin. Poultry Science 33, 100-107, 1954. 101
- JUKES, T. H., Prevention of perosis by choline. Journal of Biological Chemistry 134, 789-790, 1940. 110
- JUKES, T. H. and E. L. R. STOKSTAD, Reproduction in chickens on synthetic B-complex supplement. Proceedings of the Society for Experimental Biology and Medicine 63, 157-158, 1946.
- JULL, M. A., Studies in hatchability. I. Hatchability in relation to antecedent egg production, fertility, and chick mortality. Poultry Science 7, 195-215, 1927-1928. 117, 127, 197
- JULL, M. A., Studies in hatchability. II. Hatchability in relation to the consanguinity of the breeding stock. Poultry Science 8, 219-229, 1928-1929a. 174
- JULL, M. A., Studies in hatchability. III. Hatchability in relation to coefficients of inbreeding. Poultry Science 8, 361-368, 1928-1929b. 174, 175
- JULL, M. A., Studies in hatchability. IV. The effect of intercrossing inbred strains of chickens on fertility and hatchability. Poultry Science 9, 149-156, 1929-1930. 174
- JULL, M. A., Studies in hatchability. VI. Hatchability in relation to current egg production. Poultry Science 10, 327-331, 1930-1931. 118, 119

- JULL, M. A., The inheritance of hatchability. Report of Proceedings of the 4th World's Poultry Congress at the Crystal Palace, London, England; July 22-30, 1930, 172-178, 1931. 179, 182
- JULL, M. A., Reproductive ability and viability of progeny in relation to age of sires and dams. *Poultry Science* 14, 105-111, 1935. 115
- JULL, M. A., *Poultry Breeding*, 2nd ed., New York (John Wiley and Sons), 1940. 182
- JULL, M. A. and S. HAYNES, Shape and weight of eggs in relation to their hatching quality. *Journal of Agricultural Research* 31, 685-694, 1925. 68, 71, 74
- JULL, M. A., M. G. McCARTNEY and H. M. EL-IBIARY, Hatchability of chicken and turkey eggs held in freezing temperatures. *Poultry Science* 27, (Abstract: 26, 545-546, 1947), 136-140, 1948. 51
- KALLAI, L., B. AROS, F. BISZKUP and U. P. KRALOVÁNSZKY, Der Einfluss von Vitamin B₁₂ auf die Eierproduktion und Brutfähigkeit. *Acta Agronomica Academiae Scientiarum Hungaricae* 5, 441-449, 1956. 100
- KALTOFEN, R. S., Hatching experiments at Beckbergen - Turning the eggs. *World's Poultry Science Journal* 1955, pp. 204-209. 63
- KALTOFEN, R. S., Der Einfluss des Befruchtungsprozentsatzes und der Häufigkeit des Wendens auf die embryonale Sterblichkeit während der künstlichen Brut. *Archiv für Geflügelkunde* 22, 289-327, 1958. 63
- KALTOFEN, R. S. and P. UBBELS, Over het keren der eieren bij machinaal broeden. *Instituut voor Veeteelkundig Onderzoek* 1953. 63
- KAMAR, G. A. R., The influence of semen characteristics on hatching results of chicken eggs. *Poultry Science* 39, 188-192, 1960.
- KARAPETYAN, S. K., Eksperimentalnye dannye o vliyanií periodicheskí izmenyaemogo termicheskogo rezhima na vyzhivaenost embriona kur (Experimental data on the effect of periodic changes of thermal regimen on hen embryo survival). *Dokl. Akad. Nauk Arm. SSR* 24, 141-144, 1957. Quoted from *Biological Abstracts* 35, 2609, 1960. 50
- KARASSZON, D., Keltetéskörtani vizsgálatok (Investigations into the pathology of hatching). *Magyar Állatorvosok Lapja* 1958, pp. 197-200. 202
- KARNOFSKY, D. A., P. A. PATTERSON and L. P. RIDGWAY, Effect of folic acid, "4-amino" folic acids and related substances on growth of chick embryo. *Proceedings of the Society for Experimental Biology and Medicine* 71, 447-452, 1949. 99
- KARNOFSKY, D. A., L. P. RIDGWAY and P. A. PATTERSON, Production of achondroplasia in the chick embryo with thallium. *Proceedings of the Society for Experimental Biology and Medicine* 73, 255-259, 1950. 194
- KARNOFSKY, D. A., C. C. STOCK, L. P. RIDGWAY and P. A. PATTERSON, The toxicity of vitamin B₉, 4-desoxypyridoxine and 4-methoxymethylpyridoxine, alone and in combination, to the chick embryo. *Journal of Biological Chemistry* 182, 471-478, 1950. 98
- KATO, K. and M. FUNAHASHI, Influence of high preserving temperature upon the hatching of hens' eggs. *Journal of the Society of Tropical Agriculture, Taihoku Imperial University, Formosa, Japan* 7, 257-263, 1935. 50, 51
- KAUFMAN, L., Über den Einfluss von Temperaturen unter dem Entwicklungsminimum auf bebrütete Hühnereier. *Archiv für Entwicklungsmechanik* 131, 193-204, 1934. 56
- KAUFMAN, L., Entwicklung und Wachstum von Hühnerembryonen in frischen und in gelagerten Eiern. *Archiv für Geflügelkunde* 12, 65-77, 1938. 52
- KAUFMAN, L., An experimental study on the effects of storage on embryonal development of hens' eggs. *Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939, pp. 186-187. 53*

- KAUFMAN, L., "Aging" of eggs. II. Decrease of hatchability and catalase content in stored eggs. *Annales Universitatis Mariae Curie-Sklodowska Lublin* 2, Section E, 19-27, 1948a. 53
- KAUFMAN, L., The effect of certain thermic factors on the morphogenesis of fowl embryos. Official Report. Eighth World's Poultry Congress Copenhagen 1948. *I*, 351-356, 1948b. 56
- KAUFMAN, L. and R. GANCARCZYK, Studies on the seasonal changes in fecundity and hatchability of Polish Greenleg chickens (Polish with English summary). *Roczniki Nauk Rolniczych* 68, 109-114, 1954.
- KAUPP, B. F., The effect of shell texture on the hatchability of hens' eggs. *Poultry Item* 26, 12, 1924.
- KAUPP, B. F. and R. S. DEARSTYNE, Effect of turning eggs on hatching. Forty-ninth Annual Report, North Carolina Agricultural Experiment Station, for the year ended June 30, 1926, p. 75.
- KAWAHARA, T., A new micromelic mutant domestic fowl. National Institute of Genetics (Japan) Annual Report No. 6 for 1955, 15-16, 1956. 162
- KELLER, O., Die antike Tierwelt. Leipzig (W. Engelmann), 2, 135, 1913. 24
- KEMP, T., und J. ENGELBRETH-HOLM, Über das Vorkommen tripolarer Mitosen bei einem Hühnerembryo mit Doppelmissbildung (Cephalopagus). *Archiv für experimentelle Zellforschung* 10, 117-125, 1930. 190
- van KEMPEN, G., Note sur la vitalité du poulet dans l'oeuf. *Ornis* 11, 424, 1901.
- KENNARD, D. C., R. M. BETHKE and V. D. CHAMBERLIN, Built-up floor litter a source of dietary factors essential for hatchability of chicken eggs. *Poultry Science* 27, 477-481, 1948. 110
- KIMBALL, E., Personal communication. 168, 169
- KIMURA, I., Artificial incubation of duck eggs in Formosa: (Translated into Chinese by Ts'a Jui). *Nung-hsüeh ts'ung-shu* Shanghai nung-hsüeh hui, Shanghai, about 1900. The Gest Oriental Library, Catalogue No. 1668, series II, vol. 26. 14
- KIMURA, S. and H. ARIYAMA, On the nutritive studies of pantothenic acid by antimetabolites. II. Effect of omega-methyl pantothenic acid on the development of the chick embryo. *Tohoku Journal of Agricultural Research* 10, 237-240, 1959. 98
- KING, F. H., Farmers of Forty Centuries or Permanent Agriculture in China, Korea and Japan. 2nd edition. New York (Harcourt, Brace and Co.), 1927. 14
- KING, S. C. and J. H. BRUCKNER, A comparative analysis of purebred and cross-bred poultry. *Poultry Science* 31, 1030-1036, 1952.
- KIRCHHERR VON SUCHEN, Herrn Rudolph Kirchherrs von Suchen/etc. Fleissige Aufzeichnung aller Gelegenheit/Reysen/Gebäude/Wunder vnd anderer Werck/Gebäuden/Stätten/Wassern/Erdfrüchten/Thieren/vnd sonst allerhand Sachen/so in dem heyligen und daran angrenzenden Oertern/ von 1336 bis auff das 1350 jar vermeldt worden. Geschehen durch den Herrn Rudolphen Kirchherrn zu Suchen in Westphalen. In: S. FEYRABEND, Reyssbuch dess heyligen Lands/Das ist Ein gründtliche beschreibung aller vnd jeder Meer und Bilgerfahrten zum heyligen Lande—. Frankfort am Mayn, 1581. 19
- KIRSANOFF, Preliminary evaluation of incubator goose eggs by the color of the yolk. (In Russian). *Soviet Bird-Breeding* 1935, No. 3. Quoted from Baranchev 1936. 91
- KISH, A. F., Some observations of hatch of fertile eggs from Barred Plymouth Rocks. *Poultry Science* 27, 831-832, 1948.
- KLOSE, A. A., B. HILL and H. L. FEVOLD, Presence of a growth inhibiting substance in raw soybeans. *Proceedings of the Society for Experimental Biology and Medicine* 62, 10-12, 1946. 109

- KLUGE, F., Zur Geschichte des Brutofens. Mitteilungen der Anthropologischen Gesellschaft in Wien 40, 195-196, 1910. 19
- KNOX, C. W., Correlation studies of certain characters upon hatchability and their interrelationship. Poultry Science 6, 110-117, 1926-1927. 117, 127
- KNOX, C. W., The development and use of chicken inbreds. Poultry Science 25, 262-272, 1946. 174, 176
- KNOX, C. W. and M. W. OLSEN, The effect of tremulous air cells upon the hatchability of eggs. Poultry Science 15, 345-348, 1936. 53, 54
- KNOX, C. W., J. P. QUINN and A. B. GODFREY, Comparison of Rhode Island Reds, White Wyandottes, Light Sussex, and crosses among them to produce F₁ and three-way cross progeny. Poultry Science 22, 83-87, 1943. 175
- KOCH, A. und L. STEINKE, Über Temperatur und Feuchtigkeit bei Natur- und Kunstbrut. Archiv für Kleintierzucht 3, 153-203, 1943.
- KOCH, W., Die Beeinflussung der Brut der Hühner durch Geschlechtshormone. Züchtungskunde 10, 331-333, 1935. 107
- KOCH, W., Der Einfluss von Follikelhormon auf die Befruchtung und die Embryonalentwicklung bei Vögeln. Klinische Wochenschrift 15, 698-609, 1936. 107
- KOCH, W., Der Einfluss von weiblichem Geschlechtshormon auf Befruchtung, Entwicklung und Schlupffähigkeit der Eier. Archiv für Geflügelkunde 11, 177-202, 1937. 107
- KODINECZ, G. and B. LACZA, Ultraibolya sugarak alkalmazása a tenyésztőjések keltetésénél (The application of ultraviolet rays for hatching eggs.) Allattenyésztés 3, 257-262, 1954. 106
- KODINEZ, G. A., Der Einfluss der ultravioletten Bestrahlung auf das Schlupfergebnis der Bruteier und auf die Qualität der geschlüpften Küken. Deutsche Geflügel Zeitung 4, No. 1, 2, 1955. 106
- KOHN, F. J., Artificial incubation at high altitudes. Wyoming Agricultural Experiment Station Bulletin 169, 1930. 61
- KOLĄTAJ, A., Wpływ pigmentów karotenoidowych i witaminu A na wylęgowość jaj i wzrost piskląt. The influence of carotenoid pigments and vitamin A on the hatchability of eggs and on the growth of chickens hatched from them. Annales Universitatis Mariae Curie-Sklodowska, Sectio E 12, 489-516, 1957. 93
- KONDO, K., On turkey-chicken hybrids, with special reference to their abnormal development. (Japanese with English summary). Seibutu 2, 110-114, 1947. 167
- KONDYREV, L. V., Chetyre spuchaia urodstv pri gibridiaatsii metskoi i krupnoi porody kur. (Vier Fälle der Extremitätenmissbildungen bei den Bastarden grosser und kleiner Hünerrassen). Revue Zoologique Russe 5, 111-117, 1925. 167
- KONOPLEV, N. A., Vliianie razlichnykh kompleksov vneshnikh faktorov (temperatury, vlazhnosti i skovosti dvizheniia vozdukha) na rost i razvitie zarodysha kuritsy (The influence of various combinations of external factors - temperature, humidity and air circulation - on the growth and development of chicken embryos). Trudy Nauchno-Issledovatel'skogo Instituta Ptitsvodstva 24, Inkubatsiya, 211-221, 1954. 65
- KOSIN, I. L., Some aspects of the biological action of x-rays on cock spermatozoa. Physiological Zoology 17, 289-319, 1944. 196
- KOSIN, I. L., Abortive parthenogenesis in the domestic chicken. Anatomical Record 91, 245-249, 1945. 9
- KOSIN, I. L., Preliminary results of a study on the effect of in-vivo aging of spermatozoa on the viability of chicken embryos. Abstract, Poultry Science 26, 548, 1947. 128

- KOSIN, I. L., Parthenogenesis and abortive embryonic development in the domestic fowl. Official Report, Eighth World's Poultry Congress Copenhagen 1948, 1, 345-351, 1948. 9
- KOSIN, I. L., Studies on pre-incubation warming of chicken and turkey eggs. Poultry Science 35, 1384-1392, 1956. 50
- KOSIN, I. L., Effect of simulated airplane sounds on the reproductive functions of the male domestic chicken. Journal of Applied Physiology 12, 217-220, 1958a. 65
- KOSIN, I. L., Studies of parthenogenesis in the domestic turkey and chicken. XI Congreso Mundial de Avicultura, Mexico, D.F., 21 to 28 September, 1958b. 9
- KOTLIAROV, G. S., Vliianie otkloneniia temperatury v pervye i poslednie dni inkubatsii na vyvodimost', kurinykh iaits (The effect of temperature variations during the first days of incubation on the hatching of chicken eggs). Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936a, pp. 16-17. 56
- KOTLIAROV, G. S., Vliianie kolichstva perevorachivaniia iaits kur na rezultaty inkubatsii (Effect of the frequency of turning eggs upon the results of incubation). Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936b, pp. 17-18. 63
- KRAYEVOY, I., Experimentally induced mutations in chickens through x-rays. (Ukrainian with English summary). Academy of Sciences of the Ukrainian SSR, Institute of Zoology and Biology. Memoirs on Genetics No. 2, 109-160, 1938. 196
- KRIZENECKÝ, J., J. SAJNER, V. OREL and F. MUSIL, Detection of fertilized, infertile and nonfertilized eggs in biological control of incubation and in testing of commercial eggs (Czech with English summary). Ministerstvo Potravinářského Průmyslu, Prague, 1955. 9
- KRUEGER, W. F., G. CORRAL and J. H. QUISENBERRY, The effect of low humidity during hatching on the hatchability of chicken and turkey eggs (Abstract). Poultry Science 35, 1153-1154, 1956.
- KRUEGER, W. F., T. A. QALYUBI and J. H. QUISENBERRY, The influence of time of transfer on the hatchability of chicken eggs. (Abstract). Poultry Science 38, 1220-1221, 1959.
- KRUEGER, W. F., C. A. TIJERINA and J. H. QUISENBERRY, The effect of increased air exchange during late embryonic development on hatchability of chicken eggs. (Abstract). Poultry Science 39, 1267, 1960.
- KRÜNITZ, J. G., Article "Ausbrüten" in Oekonomische Encyklopädie oder allgemeines System der Staats-, Stadt-, Haus- und Landwirthschaft in alphabetischer Ordnung, 2nd edition. 3, 176-189, Berlin (J. Pauli), 1782.
- KRÜNITZ, J. G., Article "Huhn" in Oekonomisch-technologische Encyklopädie, oder allgemeines System der Staats-, Stadt-, Haus- und Land-Wirthschaft, und der Kunst-Geschichte, in alphabetischer Anordnung. 2nd edition. 26, 1-287, Berlin (J. Pauli), 1791. 40
- KRZANOWSKA, H., Early embryonal growth in inbred lines of Brown Leghorns and their crosses. Poultry Science 38, 1446-1455, 1959. 131, 174, 181
- KUČERA, C., Über den Einfluss der Quecksilberlampenbestrahlung auf die Entwicklung der jungen Haustiere und seine Beurteilung vom zootechnischen Standpunkte. Publications biologiques de l'École des Hautes Études Vétérinaires Brno, Tchécoslovaquie 7, 1928. 105
- KUČERA, C., Influence de l'irradiation des jeunes animaux (lapins, cobayes et poules) au moyen d'une lampe à mercure (rayons ultra-violet) et son importance zootechnique. XIVème Congrès International d'Agriculture, Bucarest 7, 8 et 10 Juin, 1929. C. I. 105
- KUCHIKOVSKAYA, E. N., Vliianie na protsess razvitiia i rezultaty inkubatsii iaits kur izmeneniia rezhima inkubirovaniia pod vlianiem izmeneniia vlazhnosti. II. Vesovye izmeneniia sostavnykh chastei iaits (The effect of changes in humidity on the processes of development and the results of incubation of chicken eggs. II. Weight changes of component parts of eggs). Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936, pp. 22-24.

- KUCHKOVSKAIA, E. N., *Sroki khraneniia iaits kur i prodolzhitel'nost' progrevaniia ikh pered otborom dlia inkubatsii* (Storage period and duration of warming of hens' eggs before selection for incubation). *Trudy Nauchno-Issledovatel'skogo Instituta Ptitsevodstva* 24, Inkubatsiya, 170-175, 1954. 186
- KUIPER, J. W. and P. UBBELS, A biological study of natural incubation and its application to artificial incubation. Official Report IXth World's Poultry Congress Paris 1951, 1, 105-112. 62, 63
- KUMANOV, S., The influence of some factors upon the fertility and hatchability of hens' eggs. Official Report. Eighth World's Poultry Congress Copenhagen 1948, 1, 320-326, 1948. 72, 122
- KURNICK, A., B. L. REID, R. L. SVACHA and J. R. COUCH, Effect of dried whey on growth, egg production and hatchability. *Journal of Nutrition* 57, 345-352, 1955.
- KURNICK, A. A., R. L. SVACHA, B. L. REID and J. R. COUCH, Further evidence for an unidentified factor required in a purified diet for normal hatchability. *Poultry Science* 35, 658-662, 1956. 110
- KUSHNER, KH. F., and O. N. KITAEVA, O merakh bor'by s otritsatel'nyimi posledstviyami inbridinga v ptitsevodstve (Measures to counteract the results of inbreeding in poultry). *Doklady Akademii Nauk SSSR* 79, 665-668, 1951. 178
- KUSHNER, KH. F., G. IA. KOREPANOVA i V. N. BUKIN, Produktivnost' i inkubatsionnye kachestva iaits u kur v zavisimosti ot pitaniia (Productivity and incubation qualities of chicken eggs as related to feeding). *Doklady Akademii Nauk S.S.S.R.* 72, 1191-1194, 1950.
- LABBE, E. H., Notes au sujet du refroidissement des oeufs pendant le cours de l'incubation. *Bulletin de la Société d'Acclimatation de France* 72, 67-76, 1925.
- LALLEMAND, S., La strophosomie chez l'embryon de poulet, réaction tératogène de la colchicine. *Archives d'Anatomie, d'Histologie et d'Embryologie* 28, 217-253, 1939. 196
- LAMOREUX, W. F., The influence of intensity of egg production upon infertility in the domestic fowl. *Journal of Agricultural Research* 61, 191-206, 1940. 126
- LAMOREUX, W. F., Hereditary chondrodystrophy in the fowl. Abstract. *Poultry Science* 20, 465, 1941. 146
- LAMOREUX, W. F., Hereditary chondrodystrophy in the fowl. *Journal of Heredity* 33, 275-283, 1942. 146-150
- LAMOREUX, W. F. and F. B. HUTT, Genetic resistance to deficiency of riboflavin in the chick. *Poultry Science* 27, 334-341, 1948. 97
- LAMSON, JR., G. H., The effects of sub-normal temperature upon the chick embryo in incubation. *Journal of the American Association of Instructors and Investigators in Poultry Husbandry* 4, 35-36, 1917-1918. 57
- LAMSON, JR., G. H., Incubation. *Transactions of the First World's Poultry Congress at the Hague-Scheveningen, September 5-9, 1921*, 1, 103-108.
- LAMSON, JR., G. H. and L. E. CARD, Factors in incubation. II. Storrs Agricultural Experiment Station Bulletin 105, 1920. 117
- LAMSON, JR., G. H. and H. D. EDMOND, Carbon dioxide in incubation. *Storrs Agricultural Experiment Station Bulletin* 76, 1914. 65
- LAMSON, JR., G. H. and W. F. KIRKPATRICK, Factors in incubation. *Storrs Agricultural Experiment Station Bulletin* 95, 1918. 49, 57, 59, 63
- LANDAUER, W., Untersuchungen über Chondrodystrophie. I. Allgemeine Erscheinungen und Skelett chondrodystrophischer Hühnerembryonen. *Archiv für Entwicklungsmechanik* 110, 195-278, 1927. 193
- LANDAUER, W., Experimental studies concerning the development of the chicken embryo. I. The toxic action of lithium and magnesium salts. *Poultry Science* 8, 301-312, 1928-1929.

- LANDAUER, W., Genetics and biology of the Creeper (Scotch Dumpie) and the Frizzle fowl. Report of Proceedings of the 4th World's Congress at the Crystal Palace, London, England: July 22-30, 1930, 128-133, 1931.
- LANDAUER, W., Studies on the Creeper Fowl. III. The early development and lethal expression of homozygous Creeper embryos. *Journal of Genetics* 25, 367-394, 1932a. 139
- LANDAUER, W., The effect of irradiating eggs with ultra-violet light upon the development of chicken embryos. Experiments with Frizzle and Creeper fowl. *Storrs Agricultural Experiment Station Bulletin* 179, 1932b. 105, 131
- LANDAUER, W., Untersuchungen über das Krüperhuhn. IV. Die Missbildungen homozygoter Krüperembryonen auf späteren Entwicklungsstadien. (Phokomelie und Chondrodystrophie). *Zeitschrift für mikroskopisch-anatomische Forschung* 32, 359-412, 1933. 139
- LANDAUER, W., Studies on the Creeper fowl. VII. The expression of vitamin D deficiency (rickets) in Creeper chicks as compared with normal chicks. *American Journal of Anatomy* 55, 229-252, 1934. 105
- LANDAUER, W., Studies on the Creeper fowl. IX. Malformations occurring in the Creeper stock. *Journal of Genetics* 30, 303-320, 1935a. 141
- LANDAUER, W., A lethal mutation in Dark Cornish fowl. *Journal of Genetics* 31, 237-242, 1935b. 141, 142
- LANDAUER, W., Micromelia of chicken embryos and newly hatched chicks caused by a nutritional deficiency. *Anatomical Record* 64, 267-276, 1936. 112
- LANDAUER, W., A lethal mutation in Japanese Bantam fowl. *Genetics* 23, 155, 1938. 139
- LANDAUER, W., Studies on the Creeper fowl. XIII. The effect of selenium and the asymmetry of selenium-induced malformations. *Journal of Experimental Zoology* 83, 431-443, 1940. 113
- LANDAUER, W., A semi-lethal mutation in fowl, affecting length of the upper beak and of the long bones. *Genetics* 26, 426-437, 1941a. 145
- LANDAUER, W., Teratological correlations and the mechanism of gene expression. Proceedings of the Seventh International Genetical Congress, Edinburgh, Scotland 23-30 August, 1939, 181-185, 1941b. 184
- LANDAUER, W., Studies on the Creeper fowl. XIV. The Japanese Bantam fowl. *American Naturalist* 76, 308-317, 1942a. 139
- LANDAUER, W., Form and function in Frizzle fowl: the interaction of hereditary potentialities and environmental temperature. *Biological Symposia* 6, 127-166, 1942b. 131
- LANDAUER, W., Sex and season in relation to malformations of chicken embryos. *Anatomical Record* 86, 365-372, 1943. 117, 170, 194
- LANDAUER, W., The results of selection against expression of the "short upper beak" mutation in fowl. *American Naturalist* 80, 490-494, 1946. 146
- LANDAUER, W., Insulin-induced abnormalities of beak, extremities and eyes in chickens. *Journal of Experimental Zoology* 105, 145-172, 1947a. 194, 196
- LANDAUER, W., Potentiating effects of adrenal cortical extract on insulin-induced abnormalities of chick development. *Endocrinology* 41, 489-493, 1947b. 194
- LANDAUER, W., The effect of nicotinamide and α -ketoglutaric acid on the teratogenic action of insulin. *Journal of Experimental Zoology* 109, 283-290, 1948a. 194
- LANDAUER, W., Hereditary abnormalities and their chemically-induced phenocopies. *Growth Symposium* 12, 171-200, 1948b. 194
- LANDAUER, W., On teratogenic effects of pilocarpine in chick development. *Journal of Experimental Zoology* 122, 469-483, 1953. 194

- LANDAUER, W., On the chemical production of developmental abnormalities and of phenocopies in chicken embryos. *Journal of Cellular and Comparative Physiology* 43, Supplement, 261-305, 1954. 196
- LANDAUER, W., Recessive and sporadic rumplessness of fowl; effects of penetrance and expressivity. *American Naturalist* 89, 35-38, 1955. 196
- LANDAUER, W., A second diplopod mutation of the fowl. *Journal of Heredity* 47, 57-63, 1956a. 157
- LANDAUER, W., Cyclopia and related defects as a lethal mutation of fowl. *Journal of Genetics* 54, 219-235, 1956b. 158-161
- LANDAUER, W., The teratogenic activity of pilocarpine, pilocarpidine and their isomers, with special reference to the importance of steric configuration. *Journal of Experimental Zoology* 132, 39-50, 1956c. 194
- LANDAUER, W., Oxidative metabolism and seasonal variations in the incidence of perocephaly of chicken embryos. *Journal of Experimental Zoology* 136, 171-183, 1957a. 67, 160
- LANDAUER, W., The primary sex ratio of fowl. *Nature* 180, 1139-1140, 1957b. 171
- LANDAUER, W., Phenocopies and genotype, with special reference to sporadically-occurring developmental variants. *American Naturalist* 91, 79-90, 1957c. 196
- LANDAUER, W., Niacin antagonists and chick development. *Journal of Experimental Zoology* 136, 509-530, 1957d. 98, 194
- LANDAUER, W., A lethal mutation in Dorking fowl. *Journal of Heredity* 50, 137-139, 1959. 160
- LANDAUER, W. and I. BAUMANN, Rumplessness of chicken embryos produced by mechanical shaking of eggs prior to incubation. *Journal of Experimental Zoology* 93, 51-74, 1943. 54
- LANDAUER, W. and C. I. BLISS, Studies on the Creeper fowl. XV. Maternal inheritance in survival of embryos from reciprocal crosses involving the Creeper factor. *Genetics* 28, 218-226, 1943. 196
- LANDAUER, W. and C. I. BLISS, Insulin-induced rumplessness of chickens. III. The relationship of dosage and of developmental stage at time of injection to response. *Journal of Experimental Zoology* 102, 1-22, 1946. 141
- LANDAUER, W. and L. C. DUNN, Chondrodystrophia in chicken embryos. *Proceedings of the Society for Experimental Biology and Medicine* 23, 562-566, 1926. 193
- LANDAUER, W. and L. C. DUNN, Studies on the Creeper fowl. I. Genetics. *Journal of Genetics* 23, 397-412, 1930a. 138
- LANDAUER, W. and L. C. DUNN, The "Frizzle" character of fowls. *Journal of Heredity* 21, 291-305, 1930b. 131
- LANDAUER, W. and A. B. LANDAUER, Chick mortality and sex-ratio in the domestic fowl. *American Naturalist* 65, 492-501, 1931. 170
- LANDAUER, W. and E. UPHAM, Weight and size of organs in Frizzle fowl. A study concerning organ adjustments following excessive loss of body heat and accelerated metabolism. *Storrs Agricultural Experiment Station Bulletin* 210, 1936. 131
- LANE, E. W., *Manners and Customs of the Modern Egyptians*. London (Ward Lock), 1836. 19
- LAU, H., *Die parthenogenetische Furchung des Hühneries*. Diss., Dorpat, 1894. 128
- LAURIE, D. F., Report of the Poultry Expert. South Australia, Report of the Department of Agriculture for the year ended June 30th, 1911, pp. 49-68. 81

- de LAVISON, R., Réponses à un questionnaire sur la fécondation des oeufs des Gallinacés. Bulletin de la Société impériale zoologique d'acclimatation 9, 366-396, 1862. 48, 53
- Le BRUYN, G., Voyage au Levant, c'est-à-dire, dans les Principaux endroits de l'Asie Mineure, dans les isles de Chio, Rhodes, Chypre, etc. De même que dans les plus considérables villes d'Egypte, Syrie, & Terre Sainte. Paris (Jean-Baptiste-Claude Bauche le fils), 1725. (First edition Delft 1700). 19
- LEMARE, Caléfacteur couvoir. Journal des connaissances usuelles et pratiques 21, 142-143, 1835. 44
- LEO AFRICANUS, J., A geographical historie of Africa, written in Arabicke and Italian by Iohn Leo a More. -- before which -- is prefixed a general description of Africa, and also a particular treatise of all the maine lands and isles vnder-described by Iohn Leo. London (G. Bishop), 1600. Original manuscript in Arabic; first published in Italian in 1550. 19
- (LEONARD), Caléfacteur économique pour faire éclore toute espèce d'oeufs. Journal des connaissances usuelles et pratiques 14, 186-187, 1831. 39, 40
- LEPKOVSKY, S., L. W. TAYLOR, T. H. JUKES and H. J. ALMQUIST, The effect of riboflavin and the filtrate factor on egg production and hatchability. Hilgardia 11, 559-591, 1938. 94, 96, 97
- LERNER, I. M., Population Genetics and Animal Improvement. Cambridge (University Press), 1950. 116
- LERNER, I. M., Genetic Homeostasis, New York (Wiley), 1954. 176
- LERNER, I. M., The Genetic Basis of Selection. New York (John Wiley & Sons), 1958. 170
- LERNER, I. M. and C. A. GUNNS, Egg size and reproductive fitness. Poultry Science 31, 537-544, 1952. 72
- LE ROI, J.-A., Histoire de Versailles, de ses rues, places et avenues depuis l'origine de cette ville jusqu'à nos jours. Versailles (Paul Oswald), 1868. 42
- LEUTMANN, J. G., Vulcanus Famylans oder sonderbahre Feuer-Nutzung welche durch gute Einrichtung der Stuben-Ofen kan erlanget werden. Wittenberg, 1720 (Chapter XXIX, pp. 67-71, "Von einem Ofen, darinnen man junge Hünere ausbrüten kan"). 5th edition, Wittenberg and Zerbst, 1764. 35-37
- LEWER, S. H., Wright's Book of Poultry. London (Cassell and Company), no date (1911). 46
- LEWIS, H. R., Report of the poultry husbandman. Thirty-second Annual Report of the New Jersey State Agricultural Experiment Station for the year ending October 31st, 1911, pp. 89-155, 1912. 58
- LEWIS, H. R., The amount and causes of embryo mortality. Forty-first Annual Report, New Jersey State Agricultural Experiment Station, for the year ending June 30, 1920, pp. 112-116.
- LEWIS, H. R. and W. C. THOMPSON, Report of the poultry husbandman. Thirty-fifth Annual Report of the New Jersey State Agricultural Experiment Station for the year ending October 31st, 1914, pp. 99-139, 1915. 133
- LEYDOLPH, W. and R. SCHNEIDERHÖHN, Zusammenhang der Schalenbeschaffenheit von Hühnereiern mit dem Schlupfergebnis. Zeitschrift für Tierzüchtung und Züchtungsbiologie 60, 331-340, 1952. 75
- LHARZIK, F., Das Gesetz des menschlichen Wachstumes und der unter der Norm zurückgebliebene Brustkorb als die erste und wichtigste Ursache der Rhachitis, Scrophulose und Tuberculose. Wien (C. Gerold's Sohn), 1858. 62
- LILLIE, R. J. and H. R. BIRD, Effect of antibiotic supplements upon hatchability and upon growth and viability of progeny. Poultry Science 31, 513-518, 1952. 101

- LILLIE, R. J., G. F. COMBS and G. M. BRIGGS, Folic acid in poultry nutrition. I. The critical need for folic acid by laying pullets. *Poultry Science* 29, 115-121, 1950. 99
- LILLIE, R. J., C. A. DENTON, M. W. OLSEN and H. R. BIRD, Vitamin B₁₂ assay methods and role in reproduction in chickens. Abstracts of Papers, 116th Meeting, American Chemical Society, p. 37A, 1950. 100
- LILLIE, R. J., M. W. OLSEN and H. R. BIRD, Role of vitamin B₁₂ in reproduction of poultry. *Proceedings of the Society for Experimental Biology and Medicine* 72, 598-602, 1949. 100, 110
- LILLIE, R. J., M. W. OLSEN and H. R. BIRD, Variation in reproductive response of hens to dietary deficiency. *Poultry Science* 30, 92-97, 1951. 92
- LINDSTROM, R. G., P. R. MOORE, C. F. PETERSEN and A. C. WIESE, Activity of a vitamin B₁₂ concentrate for chick growth and hatchability. *Poultry Science* 28, 464-465, 1949. 100
- LINDSTROM, R. G., C. F. PETERSEN, A. C. WIESE and P. R. MOORE, Effect on hatchability of fish meal fed to hens deficient in the unidentified hatchability factor. *Poultry Science* 28, 552-555, 1949. 100
- LIPSCOMB, A. A. and A. E. BERGH, *The Writings of Thomas Jefferson*. Monticello edition. Washington (Thomas Jefferson Memorial Association), 1904, vol. 13, pp. 176-177. 42
- LISSOT, G., Incubation artificielle. *Annales de la Nutrition et de l'Alimentation* 8, 143-171, 1954.
- LISSOT, G. et F. CARIDROIT, Rôle de la vitamine A dans la faculté d'éclosion des oeufs. *Bulletin de la Société de Chimie Biologique* 23, 201-204, 1941. 93
- LITHGOW, W., *The Totall Discourse, of the Rare Aduentures, and painefull peregrinations of long nineteene Yeares Trauayles, from Scotland, to the most Famous Kingdomes in Europe, Asia and Affrica*. London (Nicholas Okes), 1632. Reprinted: Glasgow (J. MacLehose and Sons), 1906. 17
- LITTLE, R. J. and W. C. THOMPSON, A comparison of two calcites as calcium supplements to the feed of laying hens. *Poultry Science* 26, 223-228, 1947. 111
- LORENZ, F. W. and W. E. NEWLON, Influence of avian pneumoencephalitis on subsequent egg quality. *Poultry Science* 23, 193-198, 1944. 202
- LUCAS, *Voyage du Sieur Paul Lucas fait en M. DCCXIV, & c. par ordre de Louis XIV dans la Turquie, l'Asie, Sourie, Palestine, Haute et Basse Egypte, & c.* Amsterdam, 1720. 19
- LUCAS, H. L., L. C. NORRIS and G. F. HEUSER, Observations on the choline requirements of hens. *Poultry Science* 25, 373-375, 1946. 110
- LUCAS, J. M. S., The effect of Nicarbazin on growth rate, sexual maturity, egg production, fertility and hatchability. *Journal of Comparative Pathology and Therapeutics* 68, 300-307, 1958. 136
- LUCRETIUS, *Of the Nature of Things*. Translated by W. E. Leonard. New York (E. P. Dutton), 1950. 19
- LYONS, M. and W. M. INSKO, JR., Chondrodystrophy in the chick embryo produced by a mineral deficiency in the diet of the hen. *Science* 80, 328, 1937. 111
- LYONS, M. and W. M. INSKO, JR., Chondrodystrophy in the chick embryo produced by manganese deficiency in the diet of the hen. *Kentucky Agricultural Experiment Station Bulletin* 371, 1937. 111
- MCCARTNEY, M. G. and C. S. SHAFFNER, Chick thyroid size and incubation period as influenced by thyroxine, thiouracil and thyroprotein. *Poultry Science* 28, 223-228, 1949. 112, 113, 133
- MCCARTNEY, M. G. and C. S. SHAFFNER, The influence of altered metabolism upon fertility and hatchability in the female fowl. *Poultry Science* (Abstract 28, 773-774, 1949) 29, 67-77, 1950. 133

- McCLYMONT, G. L. and L. HART, Studies on nutrition of poultry. I. Investigations on the inadequacy of high wheat content ratios for hatchability in White Leghorn pullets. *Australian Veterinary Journal* 23, 247-253, 1947. 97, 108
- McCLYMONT, G. L. and L. HART, Studies on nutrition of poultry; investigations on the effect of vitamin A deficiency on hatchability and egg production. *Australian Veterinary Journal* 24, 5-12, 1948. 93
- McCONACHIE, J. D., C. M. HUNTSMAN and F. N. JEROME, Relation between rate of growth and length of incubation period (Abstract). *Poultry Science* 31, 926, 1952.
- McCONACHIE, J. D., F. N. JEROME and W. F. PEPPER, The effect of pre-incubation treatments on the hatchability of chicken eggs. *Poultry Science* 39, 886-889, 1960. 50
- McCUE, J. J., Incubators and incubation. *Agricultural Gazette of New South Wales* 9, 538-545, 1898.
- McCUE, J. J., Eggs and incubation. *Agricultural Gazette of New South Wales* 11, 115-126, 1900a.
- McCUE, J. J., The hatching season. *Agricultural Gazette of New South Wales* 11, 571-577, 1900b. 81
- McDONALD, M. W., Methionine supplements in chicken diets. II. A breed difference in growth response to DL-methionine. *Australian Journal of Agricultural Research* 8, 587-594, 1957. 110
- McDONALD, M. W., Methionine supplements in chicken diets. III. The biochemical difference in sulphur-amino acid metabolism between White Leghorns and Australorps. *Australian Journal of Agricultural Research* 9, 161-169, 1958. 110
- McFARLANE, W. D., H. L. FULMER and T. H. JUKES, Studies in embryonic mortality in the chick. I. The effect of diet upon the nitrogen, amino-nitrogen, tyrosine, tryptophan, cystine and iron content of the proteins and on the total copper of the hen's egg. *Biochemical Journal* 24, 1611-1631, 1930. 108
- McGIBBON, W. H., The inheritance of short lower mandible in the fowl. Abstract. *Poultry Science* 25, 406, 1946. 154
- McGINNIS, J., G. F. HEUSER and L. C. NORRIS, The need for a new unidentified factor for reproduction in chickens. Abstract. *Poultry Science* 23, 553, 1944.
- MacLAURY, D. W. and W. M. INSKO, JR., Effect of "infertiles" and "early dead" on embryo mortality in adjacent eggs. *Poultry Science* (Abstract 26, 549, 1947) 27, 127-135, 1948.
- MacLAURY, D. W. and A. B. MORAN, Bacterial contamination of hatching eggs. *Kentucky Agricultural Experiment Station Bull.* 665, 1959. 202
- McNALLY, E. H. and T. C. BYERLY, Variation in the development of embryos of hen's eggs. *Poultry Science* 15, 280-283, 1936. 73, 123-126, 184
- McNARY, H. W. and A. E. BELL, An apparent maternal embryonic growth depressant in chickens (Abstract). *Poultry Science* 36, 1139-1140, 1957. 97
- MAFFEY, J., The examination of dead-in-shell chicks in the diagnosis of hatch failure. *State Veterinary Journal* 10, 1955.
- MAGALOTTI, L., Saggi di naturali esperienze fatte nell' Accademia del cimento sotto la protezione del serenissimo principe Leopoldo di Toscana e descritte dal segretario di essa accademia. Firenze (Giuseppe Cocchini), 1667. 22
- MAGAUD d'AUBUSSON, L'incubation artificielle en Égypte. *Bulletin de la Société Nationale d'Acclimatation de France* 57, 147-151, 1910.
- MALLMANN, W. L. and J. M. MOORE, Studies of pullorum disease. II. The incidence of *Salmonella pullorum* in eggs from infected hens. *Journal of the American Veterinary Medical Association* 89, 35-52, 1936. 200, 201

- MANCINI, E., Effetti delle basse temperature sulle uova. Premier Congrès International du Froid, Paris 2, 753-754, 1908. 51
- MANDEVILLE, The Buke of John Maundeuell being the Travels of Sir John Mandeville, Knight 1322-1356. A hitherto unpublished English Version from the unique copy (Egerton Ms. 1882) in the British Museum. Westminster (Nichols and Sons), 1889. 18, 19
- MANDEVILLE, The Travels of Sir John Mandeville. London (Macmillan and Co.), 1915. 18, 19
- MARBLE, D. R., J. A. HARPER and E. V. HAMMERS, Inheritance in the domestic fowl of a lethal condition affecting both mandibles. Poultry Science (Abstract 21, 474, 1942) 23, 114-117, 1944. 152, 153
- MARCHLEWSKI, JR., Guinea fowl (*Numida meleagris* L.) and common fowl (*Gallus domesticus* L.) hybrids obtained by means of artificial insemination. Bulletin International de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles, B: Sciences Naturelles (II) 1936; pp. 127-130. 168
- MARIAKULANDAI, A. and J. MCGINNIS, The vitamin B₁₂ requirement for hatchability of chicken eggs. Poultry Science 32, 3-7, 1953. 101
- MARIAKULANDAI, A., T. MYINT and J. MCGINNIS, Effect of terramycin and vitamin B₁₂ on hatchability. Proceedings of the Society for Experimental Biology and Medicine 79, 242-244, 1952. 101
- MARSHALL, W., The relationship of visceral anomalies of full term dead-in-shell to embryonic malposition. Official Report. Eighth World's Poultry Congress Copenhagen 1948, 1, 336-341, 1948.
- MARSHALL, W., Abnormalities of the heart and great vessels in full term dead-in-shell embryos. Official Report IXth World's Poultry Congress, Paris 1951, 1, 80-87.
- MARSHALL, W. and D. B. CRUICKSHANK, The function of the cuticle in relation to the porosity of eggs. Journal of Agricultural Science 28, 24-42, 1938. 61, 76, 81
- MARTIN, J. H., S. E. ERIKSON and W. M. INSKO, JR., The effect of vitamin D supplements on laying hens. Kentucky Agricultural Experiment Station Bulletin 304, 1930. 103
- MARTIN, J. H. and W. M. INSKO, JR., The effect of vitamin D supplement on hatchability. Proceedings of Twenty-first Annual Meeting, Poultry Science Association 1929. Bulletin of Alabama Polytechnic Institute 25, 38-43, 1930. 103
- MARTIN, J. H. and W. M. INSKO, JR., Cod liver oil for laying pullets. Kentucky Agricultural Experiment Station Bulletin 337, 1933. 103
- MARTIN, J. H. and W. M. INSKO, JR., Relationship between age, fecundity and hatchability. Poultry Science 13, 188-190, 1934. 115
- di MARTONI, N., Liber peregrinationis ad loca sancta ed. by Léon Le Grand. Revue de l'Orient latin 3, 566-669, 1895. 19
- MASHTALER, G. A., Biologiya ptits i vopros'i ptitsevodstva (Biology of birds and the problem of bird breeding). Priroda (Moscow) 1948, No. 12, pp. 36-41. 57
- (MATHIEU), De l'incubation artificielle, ou de la pratique de faire éclore les oeufs par milliers, considérée sous des rapports administratifs; par un ancien administrateur. In: Du régime des mœurs, considéré sous des rapports administratifs, ou quelque aperçus sur le véritable caractère des institutions auxquelles l'Égypte est redevable de la stabilité de ses succès dans l'exploitation de ses fours à poulets; sur le danger de s'égarer dans la route à tenir pour introduire cette même industrie en France, et sur la nature des seules mesures à prendre pour en obtenir des résultats de quelque intérêt. Paris (Imprimerie d'Hacquant), 1817. 23
- MAURO, F., Il trattamento frigorifico delle uova (di Gallina) e le sua influenza sulla capacità di sviluppo della macula germinativa. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano 61, 239-246, 1922. 51

- MAW, A. J. G., Inherited riboflavin deficiency in chicken eggs. *Poultry Science* 33, 216-217, 1954. 97
- MAYFIELD, H. I., L. M. ODLAND, L. PAGE and E. R. HALBROOK, Egg quality as influenced by certain feed combinations. Montana Agricultural Experiment Station Technical Bulletin 493, 1953. 97
- MAYR, E., Beobachtungen über die Brutbiologie der Grossfusshühner von Neuguinea (Megapodius, Talegallus und Aepypodius). *Ornithologische Monatsberichte* 38, 101-106, 1930. 5
- MEALL, L. A., Moubray's Treatise on Domestic and Ornamental Poultry. New edition. London (Arthur Hall, Virtue and Co.), 1854. 47
- MEHRING, JR., A. L., H. W. TITUS and J. WADDELL, The effect of adding methionine and vitamin B₁₂, singly and together, to a corn-soybean diet for laying chickens. *Poultry Science* 33, 1191-1197, 1954. 100, 110
- MEIRELLES de MIRANDA, R., Estudo dos resultados da incubação de ovos produzidos e fecundados por reprodutores de diversas idades. Publication 15, Instituto de Zootecnia, Ministerio da Agricultura, Rio de Janeiro, Brazil, 1956. 116, 117
- MELENDY, J. W., F. X. OGASAWARA and W. O. WILSON, Fertility and hatchability of chicken eggs produced by hens with induced hyperthermy. *Poultry Science* 38, 982-983, 1959. 133
- MELLEN, W. J., Hereditary exencephaly in the fowl (Abstract). *Poultry Science* 35, 1158, 1956.
- MELTON, E., Eduward Meltons, Engelsch Edelmans, Zeldsaame en Gedenkwaardige Zee-en Land-Reizen, Amsterdam (Jan ten Hoorn), 1681. 19
- MESHEW, M. H., The use of oxygen in the hatching of chicken and turkey eggs at high altitudes. *Poultry Science* (Abstract 27, 675, 1948) 28, 87-97, 1949. 61
- MEYER, O., Untersuchungen an den Eiern von Megapodius eremita. *Ornithologische Monatsberichte* 38, 1-5, 1930a. 5
- MEYER, O., Über die Dauer der Embryonalentwicklung bei Megapodius eremita. *Ornithologische Monatsberichte* 38, 6-7, 1930b. 5
- MEYER, O. und E. STRESEMANN, Zur Kenntnis der Entwicklung von Megapodius und Oxyura im Ei. *Ornithologische Monatsberichte* 36, 65-71, 1928. 5
- MILBY, T. T. and D. H. SHERWOOD, The influence of pre-incubation treatment on hatchability of chicken and turkey eggs. *Poultry Science* 39, 1118-1121, 1960. 50
- MILLEY, T. T. and D. H. SHERWOOD, Influence of pre-incubation treatment on hatchability of chicken and turkey eggs. (Abstract). *Poultry Science* 38, 1229, 1959.
- MILLIGAN, J. L., G. H. ARSCOTT and G. F. COMBS, Vitamin B₁₂ requirement of New Hampshires. I. Requirement of laying pullets. *Poultry Science* 31, 595-603, 1952. 101
- MILLIGAN, J. L. and G. F. COMBS, Vitamin B₁₂ requirements for hatchability, viability and growth. Abstract. *Poultry Science* 29, 772, 1950. 100
- MITSUMOTO, T., An attempt to produce quail-chicken hybrids. *Tohoku Journal of Agricultural Research* 10, 59-63, 1959. 168
- MIZUMA, Y., Studies on the effect by the embryonic environment on the characters of chickens. I. The influence of albumen exchange in poultry egg on hatchability. *Tohoku Journal of Agricultural Research* 10, 43-57, 1959.
- MODEBE, A. N. A. and D. H. HILL, Fertility, hatchability and egg production of poultry at University College, Ibadan. *World's Poultry Science Journal* 16, 47-55, 1960.

- MONCONYS. *Journal des Voyages de Monsieur de Monconys, conseiller du Roy en ses conseils d'Estat & Priuë & Lieutenant Criminel au Siege Presidial de Lyon. Où les Sçauants trouueront vn nombre infini de nouueautez, en Machines de Mathematique, Experiences Physiques, Raisonnemens de la belle Philosophie. Curiositez de Chymie, & conuersations des Illustres de ce siecle; outre la description de diuers Animaux & Plantes rares, plusieurs Secrets inconnus pour le Plaisir & la Santé, les Ourages des Peintres fameux, les Coûtumes & Moeurs des Nations, & ce qu'il y a de plus digne de la connoissance d'un honeste Homme dans les trois Parties du Monde. Premiere Partie. Voyage de Portugal, Prouence, Italie, Egypte, Syrie, Constantinople & Natolie. Lyon (H. Boissart & G. Remevs), 1665. 19*
- MONTANARI, G., *L'astrologia convinta di falso. Col mezzo di nuove esperienze, e regioni fisico-astronomiche, o' siu la caccia del frugnuolo. Venetia (Francesco Nicolini), 1685. 19, 31, 36, 46*
- MONTAUBAN, M. W., *A Guide to Profitable Industry; or, the Success of Artificial Incubation. London (Ward, Lock & Co.), 1881. 44*
- MONTEMAYOR, M. R., *Preliminary observations on the relationship between production, fertility, and hatchability of eggs. Philippine Journal of Animal Industry 3, 467-476, 1936. 127*
- MOOKERJEE, S., *Effects of temperature-fasting on the structural organisation of chick embryos. Archiv für Entwicklungsmechanik 146, 537-543, 1953. 48*
- MOORE, C. H., *Time interval between successive eggs and its effect on hatchability. (Abstract). Poultry Science 38, 1230-1231, 1959.*
- MORAN, T., *The effect of low temperature on hens' eggs. Proceedings of the Royal Society of London B 98, 436-456, 1925. 50*
- MORE, T., *A frutefull pleasaunt & wittie worke, of the beste state of a publique weale, and of the newe yle, called Utopia. Translated by Raphe Robynson. Second edition. London (A. Uele), 1556. (First edition 1551. Latin original: Libellus vere aureus nec minus salutaris quam festiuis de optimo reip. statu deque noua Insula Vtopia. Louvain, Thierry Mertens, 1516). 19*
- MORENG, R. E. and R. L. BRYANT, *Effects of sub-freezing temperature-exposure on the chicken embryo. I. Survival and subsequent growth up to time of hatch. Poultry Science 33 (Abstracts: 31, 928, 1952; 32, 917, 1953) 33, 855-863, 1954a. 57*
- MORENG, R. E. and R. L. BRYANT, *Effects of sub-freezing temperature-exposure on the chicken embryo. II. Hatchability, chick weight and survival to six weeks. Poultry Science 33, 987-991, 1954b. 57*
- MORENG, R. E. and R. L. BRYANT, *The tolerance of the chicken embryo to periods of low temperature exposure. Poultry Science 34, 1342-1348, 1955. 57*
- MORENG, R. E. and R. L. BRYANT, *The resistance of the chicken embryo to low temperature exposure. Poultry Science 35, 753-757, 1956. 57*
- MORENG, R. E. and C. S. SHAFFNER, *Lethal internal temperature for the chicken from the fertile egg to the mature bird. Poultry Science (Abstract: 29, 772, 1950) 30, 255-266, 1951.*
- MORIMOTO, H., S. HIZIKURO and S. ARIYOSHI, *Riboflavin metabolism in laying hens. 1. The effects of various riboflavin levels in the feed on egg production, hatchability, and riboflavin contents of eggs, blood and tissues of chickens. Bulletin of the National Institute of Agricultural Sciences, Chiba, Japan, Series G, No. 13, 122-129, 1957. 95*
- MORITA, S., *Die künstliche Erzeugung von Einzelmissbildungen, von Zwillingen, Drillingen und Mehrlingen im Hühnerei. Anatomischer Anzeiger 82, 81-102, 1936. 196*
- MORITA, S., *Die künstliche Erzeugung von Mehrfachbildungen im Hühnerei. (Durch Spaltung der Keimscheibe und durch Einführen von dem Tiere nicht entstammenden Substanzen). Anatomischer Anzeiger 84, 81-88, 1937. 196*
- MORRIS, J. A. and F. SKALLER, *Single crossing between White Leghorn and Australorp. Australian Journal of Agricultural Research 9, 842-851, 1958. 182*

- MOUBRAY, B., A practical treatise on breeding, rearing and fattening all kinds of domestic poultry, pheasants, pigeons, and rabbits; with an account of the Egyptian method of hatching eggs by artificial heat. 2nd edition. London (Sherwood, Neely and Jones), 1816. 19
- MOXON, A. L., Alkali disease or selenium poisoning. South Dakota Agricultural Experiment Station Bulletin 311, 1937. 113
- MOXON, A. L. and W. O. WILSON, Selenium-arsenic antagonism in poultry. Poultry Science 23, 149-151, 1944. 113
- MUELLER, C. D. and H. M. SCOTT, The porosity of the egg-shell in relation to hatchability. Poultry Science 19, 163-166, 1940. 84
- MULLER, H. D., R. E. MORENG and P. A. THORNTON, Response of the avian embryo to X-ray irradiation. (Abstract). Poultry Science 38, 1232, 1959.
- MULLER, Z., Effect of procaine penicillin G on performance of hens. Poultry Science 37, 1299-1303, 1958. 101
- MUNDAY, R. A., The position in the shell and weight of eighteen- to twenty-one-day chick embryos in relation to hatchability. Poultry Science 32, 202-207, 1953. 192
- MUNRO, S. S., Chondrodystrophy in fowl embryos. Scientific Agriculture 13, 97-109, 1932. 193
- MUNRO, S. S., The relation of specific gravity to hatching power in eggs of the domestic fowl. Scientific Agriculture 21, 53-62, 1940. 85, 86
- MUNRO, S. S., Further data on the relation between shell strength, potential hatchability and chick viability in the fowl. Scientific Agriculture 22, 698-704, 1942. 86
- MUNRO, S. S., Relative influence of heredity and environment on fertility and hatchability in Wyandottes. Empire Journal of Experimental Agriculture 14, 25-30, 1946. 131
- MUNRO, S. S. and I. L. KOSIN, Proof of the existence of pre-oviposital embryonic deaths in chickens and their bearing on the relation between "fertility" and hatchability. Canadian Journal of Research D 23, 129-138, 1945. 9, 127
- MURATA, A. and S. KATSUKI, Observation on embryonic mortality in poultry. Wissenschaftliche Berichte des VI. Weltgeflügelkongresses, 24. Juli bis 2. August 1936, Berlin and Leipzig 2, 58-62, 1936.
- MURPHY, R. R., J. E. HUNTER and H. C. KNANDEL, The vitamin D requirements of growing chicks and laying hens. Pennsylvania Agricultural Experiment Station Bulletin 303, 1934. 103
- MURPHY, R. R., J. E. HUNTER and H. C. KNANDEL, The vitamin D requirements of growing chicks and laying hens. Pennsylvania Agricultural Experiment Station Bulletin 334, 1936. 103
- MURRAY, JR., H. A., Physiological ontogeny. A. Chicken embryos. II. Catabolism. Chemical changes in fertile eggs during incubation. Selection of standard conditions. Journal of General Physiology 9, 1-37, 1925. 85
- MUSSEHL, F. E., Effect of manganese and iodine conditions in a specific ration for laying hens. Nebraska Agricultural Experiment Station Circular 76, 1944.
- MUSSEHL, F. E. and P. BANCROFT, Effect of low temperatures on hatching power of hens' eggs. Poultry Science 4, 79-81, 1924-1925. 51, 133
- MUSSEHL, F. E. and D. L. HALBERSLEBEN, Influence of the specific gravity of hens' eggs on fertility, hatching power and growth of chicks. Journal of Agricultural Research 23, 717-720, 1923. 85
- MYLLER, A. M., Peregrinus in Jerusalem. Fremdling zu Jerusalem oder ausführliche Reiss-Beschreibungen, worinnen P. Angelicus Maria Myller, Ordens der Diener Unser Lieben Frauen, Böhmischer Provinz etc. Seine fünf Haupt-Reisen, die er in Europa, Asia und Africa vor einigen Jahren gethan und unter Gottes Schutz glücklich vollendet hat, richtig erzehlet. Wien und Nürnberg (Peter Conrad Monath), 1735. 19

- NABER, E. C., J. K. BLETNER and S. P. TOUCHBURN, Effect of certain toxic fats and their derivatives on growth, reproductive performance, embryonic development and health of chickens (Abstract). *Poultry Science* 37, 1229, 1958. 110
- NABER, E. C., W. W. CRAVENS, C. A. BAUMANN and H. R. BIRD, The effect of thiamine analogs on embryonic development and growth of the chick. *Journal of Nutrition* 54, 579-591, 1954. 94
- NABER, E. C. and J. E. DUNN, A partial reversal of beta aminopropionitrile toxicity by pantothenic acid in the developing chick embryo and turkey poult. (Abstract). *Poultry Science* 38, 1232, 1959. 109
- NABER, E. C. and C. L. MORGAN, Studies on a hatchability depressing factor in cottonseed oil. *Poultry Science* 36, 429-431, 1957. 109
- NABER, E. C., E. S. SNELL and W. W. CRAVENS, Effect of nucleic acid derivatives in the reversal of aminopterin inhibition in the chick embryo. *Proceedings of the Society for Experimental Biology and Medicine* 81, 20-23, 1953.
- NALBANDOV, A. and L. E. CARD, Effect of the stale sperm on fertility and hatchability of chicken eggs. *Poultry Science* 22, 218-226, 1943. 128
- NEEDHAM, J., *Chemical Embryology*, 3 vols. Cambridge (University Press), 1932. 200
- NEEL, J. K., A calibration of the development of the chick under improved conditions of incubation and the relationship of developmental rate to age of hen and hatchability record. *Poultry Science* 21, 294-300, 1942. 116, 184
- NEHER, B. H. and R. M. FRAPS, Fertility and hatchability of the prematurely ovulated hen's egg. *Journal of Experimental Zoology* 101, 83-89, 1946.
- NELLI, G. C., *Saggio di Storia Letteraria Fiorentina del Secolo XVII scritta in varie lettere*. Lucca (V. Giuntini), 1759. 19
- NELSEN, O. E., Increased atmospheric pressure and development of the chick embryo. I. The effect of pressure on hatchability. *Anatomical Record* 96, Abstracts American Society of Zoologists, Forty-third annual meeting p. 72, 1946a. 64
- NELSEN, O. E., Increased oxygen pressure and the development of the chick embryo. I. The effect of increased oxygen pressure and survival. *Anatomical Record* 96, Abstracts American Society of Zoologists, Forty-third annual meeting p. 72, 1946b. 64
- NELSEN, O. E., Increased oxygen pressure and development of the chick embryo. II. The effect of increased partial pressure of oxygen upon hatchability. Abstracts American Society of Zoologists, Forty-fourth Annual Meeting. *Anatomical Record* 99, no. 4, p. 93, 1947. 64
- NELSEN, O. E., The effects of increased atmospheric pressures upon early chick development. *Journal of Morphology* 96, 359-380, 1955.
- NELSEN, O. E., The development of the primitive streak and early chick embryo in relation to low O_2 pressure. *Growth* 22, 109-124, 1958. 64, 67
- NESTLER, R. B., Comparison of cod-liver oil and ultraviolet irradiation as sources of vitamin D for confined laying hens. *Journal of Agricultural Research* 54, 571-582, 1937. 103
- NESTLER, R. B., T. C. BYERLY, N. R. ELLIS and H. W. TITUS, A new factor, not vitamin G, necessary for hatchability. *Poultry Science* 15, 67-70, 1936.
- NEW, D. A. T., A critical period for the turning of hens' eggs. *Journal of Embryology and Experimental Morphology* 5, 293-299, 1957. 63
- NEWTON, A., *A Dictionary of Birds*. London (Adam and Charles Black), 1893-1896. 169
- NICOLAIDES, C., Relation of time of laying and embryonic mortality. *Poultry Science* 12, 274-276, 1933. 120, 183
- NIEBUHR, K., *Reisebeschreibung von Arabien und anderen umliegenden Ländern*. Copenhagen, 1774-1778. English translation: Edinburgh (R. Morrison and Son), 1792. 19

- NIKOLAEVA, J. N., Vlijanie periodičeskikh podogrevov jaic pri ih hranenii na izmenija blastodiskov i rezuljaty inkubacii (The effect of periodically heating eggs during holding on changes in the blastodisc and in hatchability.) Bjull. nauč.-teh. Inform. vsesojuz. nauč.-issled. Inst. Pticev. 1958 (3), 26-30. (Quoted from Animal Breeding Abstracts 28, 329, 1960).
- NOGIER, T., Action du rayonnement gamma du radium sur les oeufs. Comptes Rendus Hebdomadaires des Séances et Mémoires de la Société de Biologie 88, 1049-1050, 1923.
- NOLLET, Leçons de Physique expérimentale. 6me ed. Paris (Durand) 4, 294, 1771. 21
- NORDEN, F. L., Voyage d'Égypte et de Nubie. Copenhague (Imprimerie de la Maison Royale des Orphelins), 1755. English translation: London, 1757. 19
- NORDSKOG, A. W., L. T. SMITH and R. E. PHILLIPS, Heterosis in poultry. 2. Crossbreds versus top-crossbreds. Poultry Science 38, 1372-1380, 1959. 175
- NORRIS, L. C., G. F. HEUSER, A. T. RINGROSE, H. S. WILGUS, JR. and V. HEIMAN, The vitamin-G requirement of poultry. Atti del V Congresso Mondiale di Pollicoltura tenutosi in Roma del 6 al 15 Settembre 1933, 2, 512-520, 1934. 94
- NORRIS, L. C., H. S. WILGUS, JR., A. T. RINGROSE, V. HEIMAN and G. F. HEUSER, The vitamin-G requirement of poultry. Cornell University Agricultural Experiment Station Bulletin 660, 1936. 94, 95
- NORTH, M. O., A review of the literature on embryonic malpositions and their effect on hatchability. U.S. Egg and Poultry Magazine 44; 224-227, 240, 242; 1938.
- NORTH, M. O., High altitude incubation of eggs. U.S. Egg and Poultry Magazine 47, 158-159, 1941. 51, 61
- NORTH, M. O., High altitude incubation of chicken and turkey eggs. Wyoming Agricultural Experiment Station Pamphlet No. 10, 1944. 61
- NORTHERN SUB-COMMITTEE of the National Poultry Institute Advisory Committee, Experiments in inbreeding poultry. Ministry of Agriculture and Fisheries (London) Bulletin 83, 1934. 174
- NOYONS, A. K. M. and P. M. H. PASCAL de HESSELLE, Über den Stoffwechsel des Hühnereies und die Bedeutung der Luftkammer. Acta Brevia Neerlandica de Physiologia, Pharmacologia, Microbiologia, c.a. 9, 170-173, 1939. 200
- OBENKO, K. S. and A. P. ANTAKOV, Vlijanie krupnosti iaits na vyvodimost' tsyplyat (The effect of egg size on hatchability of chicks). Ptitsyevodstvo 6, 34-36, 1956. 71
- OGORODNIY, Y. M., Disturbance of the water and mineral metabolism in the embryo in cases of chondrodystrophy and with a varying percentage of humidity in the air during incubation. People's Commissariat of Agriculture of the R. S. F. S. R. Scientific Research Institute of Poultry Husbandry. Material of the Study of Pathologies in Embryonic Development of Birds 2, 30-42, 1939a. 194, 200
- OGORODNIY, Y. M., The activity of the catalase and peroxidase in the blood of embryos in dependence on external factors. People's Commissariat of Agriculture of the R. S. F. S. R. Scientific Research Institute of Poultry Husbandry. Material of the Study of Pathologies in Embryonic Development of Birds 2, 43-55, 1939b. 53, 200
- OGORODNIY, Y. M., The state of the oxidising system of the blood in a chicken embryo under various conditions of development. People's Commissariat of Agriculture of the R. S. F. S. R. Scientific Research Institute of Poultry Husbandry. Material of the Study of Pathologies in Embryonic Development of Birds 2, 56-68, 1939c.

- OGORODNIY, Y. M. and E. E. PENIONSCHKEVITSCH, Role of protein and water metabolism in the pathogeny of embryonic stickiness in chicks. People's Commissariat of Agriculture of the R. S. F. S. R. Scientific Research Institute of Poultry Husbandry. Material of the Study of Pathologies in Embryonic Development of Birds 2, 5-29, 1939. 166
- OLCESE, O. and J. R. COUCH, Effect of injecting vitamin B₁₂ into eggs from hens fed a diet low in vitamin B₁₂. Poultry Science 29, 612-614, 1950. 100
- OLCESE, O., J. R. COUCH and C. M. LYMAN, The relation of unidentified factors to the nutrition of the mature domestic fowl. (Abstract) Poultry Science 28, 778, 1949. 100
- OLCESE, O., J. R. COUCH and C. M. LYMAN, Vitamin B₁₂ concentrates in the nutrition of the mature domestic fowl. Journal of Nutrition 41, 73-87, 1950. 100
- OLCESE, O., J. R. COUCH, J. H. QUISENBERRY and P. B. PEARSON, Congenital anomalies in the chick due to vitamin B₁₂ deficiency. Journal of Nutrition 41, 423-431, 1950. 100
- OLIVO, O. M., Fecondità in polli nati da uova irradiate coi raggi Roentgen e normalità dei loro discendenti. Bollettino della Società Italiana di Biologia Sperimentale 12, 589-592, 1937.
- OLSEN, M., Influence of turning and other factors on the hatching power of hens' eggs. Thesis. Iowa State College, 1930. 62
- OLSEN, M. W., Acorns one cause of olive-colored yolks. Poultry Science 21, 497-499, 1942. 108
- OLSEN, M. W., Effect of low temperature on the hatchability of eggs from various standardbred and crossbred chickens. Poultry Science 30, 180-183, 1951. 51
- OLSEN, M. W., Turkey-chicken hybrids. Journal of Heredity 51, 69-73, 1960. 167
- OLSEN, M. W. and T. C. BYERLY, The orientation of the embryo in the egg of the domestic fowl. Poultry Science 14, 46-53, 1935.
- OLSEN, M. W. and T. C. BYERLY, Multiple turning and orienting eggs during incubation as they affect hatchability. Poultry Science 15, 88-95, 1936. 63
- OLSEN, M. W. and T. C. BYERLY, Resistance of chicken embryos to mechanical disturbances. Journal of Agricultural Research 56, 221-226, 1938. 64
- OLSEN, M. W. and S. K. HAYNES, The effect of different holding temperatures on the hatchability of hens' eggs. Poultry Science 27, 420-426, 1948. 49
- OLSEN, M. W. and S. K. HAYNES, Egg characteristics which influence hatchability. Poultry Science 28, 198-201, 1949. 74
- OREGON Agricultural Experiment Station, 1949-50 Annual Report. Bulletin 491, p. 117, 1950. 97
- ORLOV, M., Vliianie na protsess razvitiia i rezultaty inkubatsii iaits kur izmenenii rezhima inkubirovaniia pod vlianiem izmenenii vlazhnosti. I. Rost i smertnosti embrionov i vyvodimost' (The effect of changes in humidity on the processes of development and the results of incubation of chicken eggs. 1. Growth and mortality of embryos in relation to hatching). Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936, pp. 19-22.
- ORLOV, M. V., Vliianie na protsess embrional'nozo razvitiia kur izmenenii rezhima inkubirovaniia putem povysheii i ponizhenii vlazhnosti v razlichnye periody inkubatsii (Effects of varying incubation conditions, by raising and lowering humidity at various periods, on the process of embryonic development of the chick). Sbornik Trudov Nauchno-Issledovatel'skii Institut Ptitsvodstva Narkomzema RSFSR (Publication of Scientific Research Institute for Poultry Breeding). Sel'khozgiz, 1941, pp. 212-223. 59
- ORLOV, M. V., Otkor oplodotvorenykh iaits s sil'nymi zarodyshami (The selection of fertilized eggs with vigorous embryos). Trudy Nauchno-Issledovatel'skogo Instituta Ptitsvodstva 24, Inkubatsiya, 156-169, 1954. 136

- O'ROURKE, W. F., H. R. BIRD, P. H. PHILLIPS and W. W. CRAVENS, The effect of low phosphorus rations on egg production and hatchability. *Poultry Science* 33, (Abstract 32, 919, 1953), 1117-1122, 1954a. 111
- O'ROURKE, W. F., H. R. BIRD, P. H. PHILLIPS and W. W. CRAVENS, The phosphorus requirements of chickens. Report of Proceedings, Tenth World's Poultry Congress. Edinburgh, Scotland 13th-21st August 1954. Part II. Section Papers, pp. 167-170, 1954b. 111
- OSBECK, P., *A Voyage to China and the East Indies*. London (B. White), 1771 (Original Swedish edition: Stockholm, 1756). 13
- OTRYGAN'EV, G. K., Vliianie na protsess razvitiia i rezultaty inkubatsii iaits kur izmenenii rezhima inkubirovaniia pod vlianiem izmenenii vlazhnosti. III. Patologiya otkhodov (The effect of changes in humidity on the processes of development and the results of incubation of chicken eggs. III. Pathology of mortality). *Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936a*, pp. 24-27.
- OTRYGAN'EV, G. K., Patologicheskie sindromy kurinogo embriona i voprosy ikh klassifikatsii (Pathological syndromes of chicken embryos and their classification). *Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936b*, pp. 32-35.
- OTRYGAN'EV, G. K., Issledovanie khondrodistrofii kur (Studies on chondrodystrophy in fowl). *Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936c*, pp. 37-38. 193
- OTRYGAN'EV, G. K., Patologo-anatomicheskii kontrol' v inkubatsii (Pathological-anatomical control of incubation). *NKZ-RSFSR Nauchno-issledovatel'skii Institut Ptitsevodstva* (Scientific Research Institute for Bird Breeding, Zagorsk), 1938. 48, 193
- OTRYGAN'EV, G. K., Vliianie vlazhnosti na razvitie patologicheskikh protsessov v iaitse (The influence of humidity on pathological development in the egg). *Sbornik Trudov Nauchno-Issledovatel'skii Institut Ptitsevodstva Narkomzema RSFSR* (Publication of Scientific Research Institute for Poultry Breeding), *Sel'khozgiz*, 1941a, pp. 241-246. 60
- OTRYGAN'EV, G. K., K. boprosu teratogeneza ektopii y ptits (On the question of the teratogenesis of ectopia in birds). *Sbornik Trudov Nauchno-Issledovatel'skii Institut Ptitsevodstva Narkomzema RSFSR* (Publication of Scientific Research Institute for Poultry Breeding), *Sel'khozgiz*, 1941b, pp. 247-250. 195
- OTRYGAN'EV, G. K. and E. N. KUCHKOVSKAIA, Diferentsirovanie rezhima inkubirovaniia kurinykh iaits v pervye piat' dney inkubatsii (Differentiation of factors of incubation during the first five days of development of chicken eggs). *Sbornik Trudov Nauchno-Issledovatel'skii Institut Ptitsevodstva Narkomzema RSFSR* (Publication of Scientific Research Institute for Poultry Breeding), *Sel'khozgiz*, 1941. pp. 232-241. 60, 195
- OTRYGAN'EV, G. K. and V. I. PEREVERENKO, Asfiksii kurinogo embriona (Asphyxiation of chicken embryos). *Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936*, pp. 35-37.
- OTT, W. H., S. KUNA, C. C. PORTER, A. C. CUCKLER and D. E. FOGG, Biological studies on Nicarbazin, a new anticoccidial agent. *Poultry Science* 35, (Abstract 34, 1215, 1955), 1355-1367, 1956. 136
- OWEN, R. D., Reciprocal crosses between the guinea and the domestic fowl. *Journal of Experimental Zoology* 88, 187-213, 1941. 167, 168
- PALAFIX, A. L., A comparison of the fertility and hatchability performance of stud and pen mated Single Comb White Leghorn pullets and cockerels. *Poultry Science* 27, 277-281, 1948.
- PALAFIX, A. L. and M. M. ROSENBERG, Dried cow manure as a supplement in a layer and breeder ration. *Poultry Science* 30, 136-142, 1951.
- PALMER, A. E. and J. M. DYKES, Improving incubation by increasing humidity. Canada Department of Agriculture, Dominion Experimental Farms Circular 42, 1927. 59

- PARIS, J. A., A memoir on the physiology of the egg, read before the Linnean Society of London, on March 21, 1809. *The Annals of Philosophy* N. S. 1, 351-359, 1821. 46
- PARKER, J. E., Relation of time of day of artificial insemination to fertility and hatchability of hens' eggs. *Poultry Science* 24, 314-317, 1945. 130
- PARKER, J. E., The effect of restricted mating in flocks of New Hampshire chickens on fertility and hatchability of eggs. *Poultry Science* 29, 268-270, 1950. 130
- PARKHURST, R. T., J. A. LABITZ, M. S. GUTOWSKA and C. R. FELLERS, The nutritive properties and use of crab meal. Abstract. *Poultry Science* 21, 475-476, 1942.
- PARMENTIER, Poule (Économie). *Nouveau Dictionnaire d'Histoire Naturelle, appliquée aux arts, principalement à l'agriculture et à l'économie rurale et domestique* 18, 425-466, Paris (Deterville), 1803. Nouvelle édition 7, 469-543, Paris (Deterville), 1817. 21
- (PARMENTIER), Incubation artificielle. *Dictionnaire technologique, ou Nouveau Dictionnaire universel des arts et métiers, et de l'économie industrielle et commerciale* 11, 160-169, Paris (Thomine), 1827. 41
- de PAUW, C., Philosophical dissertations on the Egyptians and Chinese. London (T. Chapman), 1795 (Original French edition: Amsterdam and Leyden, 1773). 19
- PAYNE, L. F., Distribution of mortality during the period of incubation. *Journal of the American Association of Instructors and Investigators in Poultry Husbandry* 6, 9-12, 1919-1920. 197
- PAYNE, L. F., A study of multiple turning of incubated eggs. *Journal of the American Association of Instructors and Investigators in Poultry Husbandry* 7, 17-19, 1920-1921.
- PAYNE, L. F. and J. S. HUGHES, The effect of inadequate rations on the production and hatchability of eggs. *Kansas Agricultural Experiment Station Technical Bulletin* 34, 1933. 93, 103
- PAYNE, L. F. and C. INGRAM, The effects of freezing the combs of breeding males. *Poultry Science* 6, 99-107, 1926-1927. 134
- PEARL, R., Inheritance of hatching quality of eggs in poultry. *American Breeders Magazine* 1, 129-133, 1910; also in Report (1909) *American Breeders Association* 6, 94-98, 1911. 182
- PEARL, R. and F. M. SURFACE, Data on certain factors influencing the fertility and hatching of eggs. *Maine Agricultural Experimental Station Bulletin* 168, 1909. 117, 127, 179
- PEARL, R. and F. M. SURFACE, A biometrical study of egg production in the domestic fowl. III. Variation and correlation in the physical characters of the egg. U. S. Department of Agriculture, Bureau of Animal Industry Bulletin 110, Part III, 1914. 74, 75
- PEELER, H. T., R. F. MILLER, C. W. CARLSON, L. C. NORRIS and G. F. HEUSER, Studies of the effect of vitamin B₁₂ on hatchability. *Poultry Science* 30, 11-17, 1951. 100
- PENJONSKHEWITSCH, E. E., Embrionalnoje Ras witije Utjat i Zipljat w swjasi s wesom jaiz. U.S.S.R. Problems of Incubation 2 (Author's abstract in *Archiv für Geflügelkunde* 10, 437-441, 1936). 72, 90
- PENJONSKHEWITSCH, E. E., Material zum Studium pathologischer Vorgänge bei der embryonalen Entwicklung des Kückens während der künstlichen Bebrütung. III. Über die Gasdurchlässigkeit der inneren Schalenhaut. *Archiv für Geflügelkunde* 11, 1-19, 1937. 88
- PENIONZHKEVICH, F. E., Problema snizheniia smertnosti embrionov domashnikh ptits (The problem of reducing embryonic mortality of domestic birds). *Ogiz sel'khozgiz*, 1945. 5, 72, 200

- PENJONSKIEWITSCH, E. E. and A. N. RETANOW, Die Bruttemperatur und ihr Einfluss auf die Entwicklung des Hühnerembryos. *Archiv für Geflügelkunde* 8, 369-383, 1934.
- PENJONSKIEWITSCH, E. E. and L. I. SCHECHTMAN, Calorimetric investigations of the embryonic development of chickens under various conditions of incubation. People's Commissariat of Agriculture of the R. S. F. S. R. Scientific Research Institute of Poultry Husbandry. Material of the Study of Pathologies in Embryonic Development of Birds 2, 76-83, 1939. 189
- PENQUITE, R., Influence of temperature and humidity upon the growth of chick embryos in a mechanically ventilated incubator. *Iowa Agricultural Experiment Station Bulletin* 232, 1938. 188
- PENSACK, J. M., R. M. BETHKE and D. C. KENNARD, The effect of fish meal and extracts of fish meal on hatchability of hens' eggs and growth of progeny. *Poultry Science* 28, 398-405, 1949. 109
- PEPPER, W. F., S. J. SLINGER, J. D. SUMMERS and G. C. ASHTON, On the phosphorus requirements of chickens for egg production and hatchability. *Canadian Journal of Animal Science* 39, 182-192, 1959.
- PERERIUS, B., De communibus omnium rerum naturalium Principijs & Affectionibus libri quindecim. Qui plurimum conferunt, non tantum ad eos octo libros, qui de Physico auditu inscribuntur, sed etiam multos alios difficilimos Aristotelis locos intelligendos. Coloniae (Lazuri Zetzneri), 1595 (first edition: Rome, 1562). 19
- PERRY, C., A View of the Levant. London (T. Woodward), 1743. 19
- PETERSEN, C. F., C. E. LAMPMAN and O. E. STAMBERG, Effect of riboflavin intake on hatchability of eggs from battery confined hens. *Poultry Science* 26, 187-191, 1947. 95
- PETERSEN, C. F., C. E. LAMPMAN and A. C. WIESE, Role of vitamin B₁₂ and other APF factors for reproduction and chick growth. Abstract. *Poultry Science* 29, 775, 1950. 100
- PETERSEN, C. F., C. E. LAMPMAN and A. C. WIESE, Use of an APF supplement with and without fish meal for egg production and hatchability. *Poultry Science* 31, 132-136, 1952. 100
- PETERSEN, C. F., A. C. WIESE, R. V. DAHLSTROM and C. E. LAMPMAN, Influence of vitamin B₁₂ and antibiotics on hatchability. *Poultry Science* 31, 129-132, 1952. 100
- PETERSEN, C. F., A. C. WIESE and C. E. LAMPMAN, The effect of several protein supplements on hatchability when fed to hens in open pens and batteries. *Poultry Science* 27, 471-476, 1948.
- PETERSEN, C. F., A. C. WIESE, C. E. LAMPMAN and R. V. DAHLSTROM, Role of crystalline vitamin B₁₂ for hatchability. *Poultry Science* 29, 618-619, 1950. 100
- PETERSEN, C. F., A. C. WIESE, G. E. MILNE and C. E. LAMPMAN, Vitamin B₁₂ requirements for hatchability and production of high-quality chicks. *Poultry Science* 32, 535-542, 1953. 101
- PFAUNDLER, L., Über zusätzliche Jodfütterung in der Geflügelzucht. *Wiener tierärztliche Wochenschrift* 27, 112-116, 1940. 112
- PHILIPS, A. G., Temperature experiments in incubation. *Purdue University Agricultural Experiment Station Bulletin* 195, 1916.
- PHILIPS, A. G., A brief study of the mating habits of fowls with a test of the value of a single mating. *Journal of the American Association of Instructors and Investigators in Poultry Husbandry* 4, 30-31, 1917-1918. 128
- PHILIPS, A. G. and F. D. BROOKS, Temperature experiments during the incubation of hen eggs. *Purdue University Agricultural Experiment Station Bulletin* 275, 1923. 55

- PHILLIPS, R. E., Hatchability as influenced by environmental and different storage temperatures. *Poultry Science* 24, 25-28, 1945. 50
- PHILLIPS, R. W., R. G. JOHNSON and R. T. MOYER, The livestock of China. Department of State Publication 2249, U.S. Government Printing Office, Washington, D.C., 1945. 16
- PICTET, R., De l'emploi méthodique des basses températures en biologie. *Archives des Sciences Physiques et Naturelles*, 3ème période 30, 293-314, 1893. 51
- PINO, J. A., Effect of washing with a hot detergent solution on keeping quality and hatchability of eggs. *Poultry Science* 29, 888-894, 1950.
- PLINY, The Historie of the World. Commonly called the Natvrall Historie of C. Pliniys Secvndvs. Translated into English by Philemon Holland. London (Adam Islip), 1601. 17
- POCOCKE, R., A description of the East, and some other countries. London, 1743-1745. 19
- POLEY, W. E. and A. L. MOXON, Tolerance levels of seleniferous grains in laying rations. *Poultry Science* 17, 72-76, 1938. 113
- POLEY, W. E., A. L. MOXON and K. W. FRANKE, Further studies of the effects of selenium poisoning on hatchability. *Poultry Science* 16, 219-225, 1937. 113
- POLK, H. D. and G. R. SIPE, The effect of vitamin A deficiency on malposition of the chick embryo. *Poultry Science* 19, 396-400, 1940. 93, 192
- PONSIGNON, M., The comb problem in White Wyandottes. Official Report IXth World's Poultry Congress, Paris 1951, 1, 70-76. 138
- PONSIGNON, M., Essai d'amélioration des facultés de fécondation et d'éclosion d'une lignée de pondeuses par le contrôle génétique. Report of Proceedings, Tenth World's Poultry Congress, Edinburgh, Scotland 13th to 21st August 1954, Part II, Section Papers, pp. 56-59, 1954.
- POOLE, H. K. and M. W. Olsen, Incidence of parthenogenetic development in eggs laid by three strains of Dark Cornish chickens. *Proceedings of the Society for Experimental Biology and Medicine* 97, 477-478, 1958. 9
- della PORTA, Magiae naturalis sive de miraculis rerum naturalium libri IIII. Io. Baptista Porta Neapolitano auctore. Neapoli (Matthias Cancer), 1558. English edition: Natural Magick. London (Thomas Young and Samuel Speed), 1658. 17, 26-28, 31
- PORTMANN, A., Die Ontogenese der Vögel als Evolutionsproblem. *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft* 1936, pp. 224-241. 5
- PORTMANN, A. and L. JECKLIN, Die Abhängigkeit der Hühnerembryonen vom Sauerstoff der Umgebung. *Schweizerisches Archiv für Ornithologie* 1, 281-286, 1936. 67
- POTTER, G. C. and F. A. KUMMEROW, Chemical similarity and biological activity of the saponins isolated from alfalfa and soybeans. *Science* 120, 224-225, 1954. 109
- POWELL, C. K., Reproductive factors influencing the interior quality of eggs. Ph.D. Thesis, Cornell University, 1925. 90
- POWELL, W., Unter den Kannibalen Neubritanniens. Leipzig, 1884. 6
- PREVOST et DUMAS, Note sur les changemens de poids que les oeufs éprouvent pendant l'incubation. *Annales des Sciences Naturelles* 4, 47-56, 1825.
- PREYER, W., Specielle Physiologie des Embryos. Leipzig (T. Grieben), 1885. 65
- PRINGLE, E. M. and H. G. BAROTT, Effect of incubation temperature on time of death of chick embryo and relationship of energy metabolism to mortality. *Journal of Agricultural Research* 54, 465-468, 1937. 200

- PRITSKER, I. IA., Razlichia v vese i vyvodospobnosti iaits, snesennykh v razlichnoe vremia dnia. (Differences in the weight and the hatchability of eggs laid during different times of the day). Doklady Vsesoiuznoi Akademii s-kh Nauk im V. I. Lenina. Prirevodstvo No. 6, 41-44, 1940a. 57, 120-122
- PRITSKER, I. IA., Vlianie vysokikh temperatur v pevye chasy incubatii na ee rezultaty. (The influence of high temperatures during the first hours of incubation). Doklady Vsesoiuznoi Akademii s-kh Nauk im V. I. Lenina. Zootekhiia No. 8, 24-28, 1940b. 50, 57
- PRITSKER, I. IA., Vlianie Uslovii Embriogeneza na ekster'er i interer odnodnevnykh tsyplyat. (The influence of embryogenesis on the exterior and interior of day-old chicks). Doklady Vsesoiuznoi Akademii s-kh Nauk im V. I. Lenina No. 4, 26-30, 1941. 57
- PRITZKER, I. J., Regularities in growth of chicken embryos. Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS N. S. 24, 823-827, 1939. 56
- PRITZKER, I. J., Über einige Modifikationen der Vogelembryonen. Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS 26, 829-932, 1940a.
- PRITZKER, I. J., Zur Frage über die Chemie des Wachstums der Vogelembryonen. Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS 28, 381-384, 1940b.
- PRUFER, J., Versuch mit der Verfütterung von Follikelhormon an Zuchthennen. Archiv für Geflügelkunde 10, 366-374, 1936. 107
- PUN, C. F., The crooked neck dwarf lethal syndrome in the domestic fowl. Journal of Experimental Zoology 126, 101-133, 1954. 153
- QUINN, J. P., W. H. BURROWS and T. C. BYERLY, Turkey-chicken hybrids. Journal of Heredity 28, 169-173, 1937. 167
- QUINN, J. P., C. D. GORDON and A. B. GODFREY, Breeding for egg shell quality as indicated by egg weight loss. Poultry Science 24, 399-403, 1945. 81
- QUISENBERRY, J. H. and R. L. ATKINSON, Effect of whole body X-ray irradiation upon the reproductive performance of White Leghorn males. Poultry Science 35, 1327-1335, 1956. 164
- RABAUD, E., De l'influence de la congélation sur le développement de l'oeuf de poule. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 128, 1183-1185, 1899. 51
- RADZIWIŁŁ, M. K., Ierosolymitana Peregrinatio Illustrissimi Principis Nicolai Christophori Radzivili. Antverpiae (Officina Plantiniana), 1614. (German edition in vol. 2 of S. FEYERABEND, Reyssbuch des Heyligen Lands—, Frankfurt a.M. 1584; Polish original published by Polska Akademia umiejtnosci, Krakowie, 1925). 19
- RAIMO, H. F., Relação entre a intensidade da cor da casca dos ovos na raça New Hampshire e os resultados da incubação. Boletim de Industria Animal N.S. 12, 95-105, 1951. 81
- RANDALL, L. M. C., A mediaeval slander. The Art Bulletin 42, 25-38, 1960. 16
- RANGLES, C. A. and A. L. ROMANOFF, Maldevelopment of the avian amnion as influenced by some environmental conditions. (Abstract) Poultry Science 28, 780-781, 1949. 64
- RANGLES, JR., C. A. and A. L. ROMANOFF, A preliminary study on the hatchability of chicken eggs subjected to shaking agitation. Poultry Science 33, 374-377, 1954. 55
- RANTZAU, H., Denckwürdige Reise-Beschreibung nach Jerusalem, Cairo in Aegypten und Constantinopel, worinnen die remarquabelsten Begebenheiten, die curieusesten Sachen, und was Er an bemeldten Oertern sonderbahres bemercket, gantz eigentlich fürgestellt werden. Hamburg (Gouffried Liebernickel), 1704. 19

- RAUCH, W., The influence of egg-shell porosity on the number of chickens hatched from incubating eggs. *Poultry Science* 31, 589-594, 1952. (also: *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 60, 1952). 79, 80
- RAUCH, W., Biophysikalische Messungen an Bruteiern. *Archiv für Geflügelkunde* 18, 297-304, 1954.
- RAUCH, W. and L. STEINKE, Über den Einfluss der Eischalenporosität und der Eischalendicke auf das Schlupfergebnis von Bruteiern. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 62, 61-66, 1953. 75, 79, 80
- de RÉAUMUR, Sur la manière de conserver les oeufs. *Histoire de l'Académie Royale des Sciences* 1735, 465-472, Paris, 1738. 50
- de RÉAUMUR, Art de faire éclore et d'élever en toute saison des oiseaux domestiques de toutes espèces, soit par le moyen de la chaleur du fumier, soit par le moyen de celle du feu ordinaire. Paris, 1749. 16, 31, 37-40, 48
- de RÉAUMUR, The art of hatching and bringing up domestic fowls of all kinds, at any time of the year, either by means of the heat of hot-beds, or that of common fire. London 1750. 16, 31, 37-40, 48
- de RÉAUMUR, Pratique de l'art de faire éclore et d'élever en toute saison des oiseaux domestiques de toutes espèces, soit par le moyen de la chaleur du fumier, soit par le moyen de celle du feu ordinaire. Paris, 1751. 39
- RECORD, P. R., R. M. BETHKE, D. C. KENNARD and V. D. CHAMBERLIN, The value of b-v riboflavin supplement for replacing dried skimmilk in an all-mash laying ration. Abstract. *Poultry Science* 21, 476-477, 1942.
- REINACH, S., Orpheus. A History of Religions. New York (Liveright), 1935. 9
- REISER, R., B. GIBSON, M. J. CARR and B. G. LAMP, The syntheses and inter-conversions of polyunsaturated fatty acids by the laying hen. *Journal of Nutrition* 44, 159-176, 1951. 108
- RESANANDA, N. T., Determination of the best season for hatching eggs in the Philippines. *The Philippine Agriculturist* 13, 81-91, 1924-1925.
- RETTGER, L. F., The bacteriology of the hen's eggs, with special reference to the freedom from microbic invasion. *Storrs Agricultural Experiment Station Bulletin* 75, 1913. 201
- RETTGER, L. F. and F. H. STONEBURN, Bacillary white diarrhea of young chicks. *Storrs Agricultural Experiment Station Bulletin* 60, 1909. 200
- RETTGER, L. F. and F. H. STONEBURN, Bacillary white diarrhea of young chicks. (Second report). *Storrs Agricultural Experiment Station Bulletin* 68, 1911. 200
- RHODES, W. F. and G. E. GODFREY, The effect of washing eggs on the cuticle as measured by moisture loss and hatchability. *Poultry Science* 29, 833-836, 1950.
- RIDDLE, O., On the necessary gaseous environment of the bird embryo. *Ecology* 5, 348-362, 1924. 65
- RIDDLE, O., Studies on the physiology of reproduction in birds. XXVII. The age distribution of mortality in bird embryos and its probable significance. *American Journal of Physiology* 94, 535-547, 1930. 200
- RINGROSE, R. C., C. L. MORGAN and E. J. LEASE, The effect of cottonseed oil on the hatchability of eggs. *Poultry Science* 20, 57-61, 1941. 109
- ROGALSKI, T., Action de l'acide carbonique sur le développement de l'oeuf de Poule. *Comptes Rendus Hebdomadaires des Séances et Mémoires de la Société de Biologie* 92, 706-708, 1925.
- ROGLER, J. C., Effects of iodine on hatchability and embryonic development. Ph.D. Thesis Purdue University, 1958. University Microfilms 58-1810. 112, 113
- ROGLER, J. C., H. E. PARKER, F. N. ANDREWS and C. W. CARRICK, The effects of an iodine deficiency on embryo development and hatchability. *Poultry Science* 38, 398-405, 1959a. 112

- ROGLER, J. C., H. E. PARKER, F. N. ANDREWS and C. W. CARRICK, Effects of thiouracil and thyroxine on chick embryo development. *Poultry Science* 38, 1027-1032, 1959b. 112, 113
- ROMANOFF, A. L., Effect of humidity on the growth, calcium metabolism, and mortality of the chick embryo. *Journal of Experimental Zoology* 54, 343-348, 1929. 59
- ROMANOFF, A. L., Biochemistry and biophysics of the developing hen's eggs. I. Influence of humidity. Cornell University Agricultural Experiment Station Memoir 132, 1930a. 59
- ROMANOFF, A. L., Effect of composition of air on the growth and mortality of the chick embryo. *Journal of Morphology and Physiology* 50, 517-525, 1930b. 65-67
- ROMANOFF, A. L., Why some eggs do not hatch. Cornell University Extension Bulletin 205, 1931.
- ROMANOFF, A. L., Study of artificial incubation of game birds. Cornell University Agricultural Experiment Station Bulletin 616, 1934. 60
- ROMANOFF, A. L., Effects of different temperatures in the incubator on the prenatal and postnatal development of the chick. *Poultry Science* 15, 311-315, 1936a. 56, 57
- ROMANOFF, A. L., Keynotes of progress in artificial incubation. *Wissenschaftliche Berichte des VI. Weltgeflügelkongresses*, 24. Juli bis 2. August 1936, Berlin und Leipzig 1, 130-141, 1936b.
- ROMANOFF, A. L., Effect of temperature shock on development of chick embryo. Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939, pp. 184-186. 188
- ROMANOFF, A. L., The increased mortality of the developing chick embryos in riboflavin-deficient eggs. Abstracts of papers. American Society of Zoologists, 38th Annual Meeting. *Anatomical Record* 78, Supplement p. 78, 1940. 194
- ROMANOFF, A. L., Recent progress in artificial incubation. Official Report. Eighth World's Poultry Congress Copenhagen 1948, 1, 43-59, 1948.
- ROMANOFF, A. L. and J. C. BAUERNFEIND, Influence of riboflavin deficiency in eggs on embryonic development (*Gallus domesticus*). *Anatomical Record* 82, 11-21, 1942. 94
- ROMANOFF, A. L. and H. A. FABER, Effect of temperature on the growth, fat and calcium metabolism, and mortality of the chick embryo during the latter part of incubation. *Journal of Cellular and Comparative Physiology* 2, 457-466, 1933. 56
- ROMANOFF, A. L. and H. W. LUDLAM, The effect of ultraviolet radiation on the hatchability of avian eggs. Abstract, American Society of Zoologists. *Anatomical Record* 87, 41, 1943. 105
- ROMANOFF, A. L. and A. J. ROMANOFF, Biochemistry and biophysics of the developing hen's egg. II. Influence of composition of air. Cornell University Agricultural Experiment Station Memoir 150, 1933. 66, 67
- ROMIJN, C., Foetal respiration in the hen. Gas diffusion through the egg shell. *Poultry Science* 29, 42-51, 1950. 60
- ROMIJN, C., Untersuchungen über künstliche Bebrütung von Hühnereiern. *Archiv für Geflügelkunde* 18; 173-183, 242-258; 1954.
- ROSENBERG, E. E., Teratogenic effects of beta-aminopropionitrile in the chick embryo. *Nature* 180, 706-707, 1957. 109
- ROSENBERG, L. E., Histological studies of muscle from crooked neck dwarf fowl. *Anatomical Record* 97, 277-282, 1947. 153
- ROSENBERG, M. M., Low-grade sugar, a potential carbohydrate feedstuff for laying chickens. *Poultry Science* 32, 69-77, 1953.

- ROSENBERG, M. M. and A. L. PALAFOX. The effect of creeping indigo. (*Indigofera endecaphylla*) on laying chickens. *World's Poultry Science Journal* 7, 9-15, 1951.
- ROSENBERG, M. M. and T. TANAKA. Egg shell color and hatchability. *Poultry Science* 30, 713-716, 1951. 81
- ROSENBLATT, L. S., G. O. KREUTZIGER and L. W. TAYLOR. Eudiplopodia. (Abstract). *Poultry Science* 38, 1242, 1959. 161, 162
- ROULLIER-ARNOULT, E. et E. ARNOULT. Notice sur les couveuses artificielles. *Bulletin Mensuel de la Société d'Acclimatation* 3e série 2, 721-731, 1875.
- ROULLIER-ARNOULT et ARNOULT. Le mirage des oeufs par l'indiscrète, leur choix et les causes principales de leur infécondité. Instruction pour l'hydro-mère. *Bulletin de la Société d'Acclimatation* 3e série 3, 729-741, 1876.
- ROULLIER-ARNOULT, et ARNOULT. Guide pratique illustré pour l'éclosion et l'élevage artificiels des oiseaux de chasse et de basse-cour par des hydro-incubateurs et hydro-mères Roullier et Arnould de Gambais-les-Houdan (Seine et Oise). 5ème édition. Paris (about 1889). 46
- ROUYER. Description particulière de plusieurs Fours à poulets observés au Kaire, et des procédés que l'on y met en usage. Description de l'Égypte ou Recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française, publié par les ordres de sa majesté l'empereur Napoléon le Grand. *Etat Moderne* 1, 211-216, Paris (Imprimerie Impériale), 1809. 19
- ROZENBAKH, I. A. Vliianie razlichnykh istochnikov vitamina B₂ na iaitsenokost' i bybodimost iaitsa kur (The influence of various sources of vitamin B₂ on the vitality and hatchability of chicken eggs). *Sbornik Trudov Nauchno-Issledovatel'skii Institut Pitsevodstva Narkomzema RSFSR* (Publication of Scientific Research Institute for Poultry Breeding), Sel'khozgiz, 1941, pp. 197-211. 94
- de ROZIÈRE. Mémoire sur l'art de faire éclore les poulets en Égypte par le moyen des fours. Description de l'Égypte ou Recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française, publié par les ordres de sa majesté l'empereur Napoléon le Grand. *Etat Moderne* 1, 203-210, Paris (Imprimerie Impériale). 1809. Reprinted as: Mémoire sur l'art de l'incubation artificielle, en Égypte, et sur les fours qu'on y employe. *Journal des Mines* 27, 145-160, 1815. 19
- RUBIN, M. and H. R. BIRD. Relation of vitamin A to egg production and hatchability. *Maryland Agricultural Experiment Station Bulletin* A 12 Technical, 1942. 93
- RUBIN, M., A. C. GROSCHKE and H. R. BIRD. Chick growth factor in cow manure. VI. Effect on hatchability and storage in hens. *Proceedings of the Society for Experimental Biology and Medicine* 66, 36-38, 1947. 110
- RUDY, W. J. and D. R. MARBLE. The interrelationship of physical measurements of eggs and their effect upon hatchability. *Poultry Science* 18, 354-358, 1939. 75, 90
- RULON, O. Differential reduction of Janus green during development of the chick. *Protoplasma* 24, 346-364, 1935. 196
- RUNNELLS, R. A. Bacillary White Diarrhea. Pullorum infection of the domestic fowl. *Virginia Agricultural Experimental Station Bulletin* 265, 1929. 200
- RUNNELLS, R. A. and H. van ROEKEL. The occurrence of white diarrhea infection in eggs laid by hens reacting to the agglutination test. *Poultry Science* 6, 141-147, 1926-1927a. 201
- RUNNELLS, R. A. and H. van ROEKEL. Further observations on the occurrence of white diarrhea infection in eggs laid by hens reacting to the agglutination test. *Poultry Science* 6, 229-232, 1926-1927b. 201
- RUSSELL, W. C., C. S. PLATT, M. W. TAYLOR and D. F. CHIDESTER. The vitamin A requirements of laying pullets. *New Jersey Agricultural Experiment Station Circular* 369, 1936. 93

- RYLE, M., Studies on possible serological blocks to species hybridization in poultry. *Journal of Experimental Biology* 34, 365-377, 1957. 168
- de SACY, S., Relation de l'Égypte, par Abd-Allatif, médecin arabe de Bagdad; suivie de divers extraits d'écrivains orientaux, et d'un état des provinces et des villages de l'Égypte dans le XIV^e siècle. Paris (Treuttel et Wurtz), 1810. 20, 21
- SADLER, W. W., H. S. WILGUS and E. G. BUSS, Incubation factors affecting hatchability of poultry eggs. 2. Some effects of carbon dioxide upon morphogenesis. *Poultry Science* 33, 1108-1115, 1954. 67
- SAEKI, Y., K. KONDO, K. HIMENO, H. IKOMA, T. KATSURAGI and Y. TANABE, Performances of F₁ progenies between S. C. White Leghorns and Japanese Nagoyas. *Bulletin of the National Institute of Agricultural Sciences Chiba, Japan, Series G*, No. 12, 79-93, 1956. 175
- SAINT-LOUP, R., Physiologie de l'embryon de poulet. Influence de la température. *Revue des Sciences Naturelles Appliquées* 37, 1017-1021, 1890.
- SAINT-LOUP, R., Les oiseaux de basse-cour. Paris (J. B. Bailliére et Fils), 1895. 12, 15
- SAINT-LOUP, R., Quelques réponses au questionnaire concernant les oeufs et l'incubation chez les oiseaux domestiques. *Ornis* 11, 421-423, 1900-1901.
- SAJNER, J., Über die mikroskopischen Veränderungen der Eischale der Vögel im Laufe der Inkubationszeit. *Acta Anatomica* 25, 141-159, 1955. 75
- SAMOLETOV, A. I., I. G. KOSTIN and M. G. SALGANNIK, Vliyanie radioaktivnykh izlucheni na process inkubacii kurinykh jaic (The effect of radioactivity on the process of incubation of hens' eggs). *Ptisevodstvo* 8, No. 11, 23-26, 1958 (*Animal Breeding Abstracts* 27, 239, 1959). 55, 164
- SANCTUARY, W. C., One cause of dead chicks in the shell. *Poultry Science* 4, 141-143, 1924-1925. 190
- SANDNES, G. C., Studies of the intergeneric hybrids of Phasianus and Gallus. Master of Science Thesis, Connecticut State College, 1937. 168
- SANDNES, G. C., Fertility and viability in intergeneric pheasant hybrids. *Evolution* 11, 426-444, 1957. 167
- SANDNES, G. C. and W. LANDAUER, The sex ratio in the cross of Phasianus torquatus ♀ x Gallus domesticus ♂. *American Naturalist* 72, 180-183, 1938. 167
- SANDVIK, Ö., The effect of chronic gamma radiation on the hatchability of chicken eggs. *Hereditas* 44, 407-414, 1958. 55, 164
- de SAUSSURE, H. B., Essais sur l'Hygrométrie. Neuchâtel (S. Fauche père et fils), 1783. 41
- SAVAGE, J. E., C. W. TURNER, H. L. KEMPSTER and A. G. HOGAN, The effects of vitamin B₁₂ and thyroprotein on egg production, egg weight, shell quality and hatchability. *Poultry Science* 31, 22-31, 1952. 100, 113
- SAVARY, C. E., Lettres sur l'Égypte, où l'on offre le parallèle des moeurs anciennes & modernes de ses habitants, où l'on décrit l'état, le commerce, l'agriculture, le gouvernement du pays, & la descente de S. Louis à Damiette, tirées de Joinville & des auteurs arabes, avec des cartes géographiques. Paris (Onfroi), 1785-1786. 19
- SAXENA, H. C. and K. KUMAR, The effect of feeding high levels of terramycin on the reproductive performance of laying hens. *Indian Veterinary Journal* 36, 578-580, 1959. 101
- van SCHALKWYK, W. R. and C. R. LIEBENBERG, The Black Australorp, the White Leghorn and their reciprocal crosses. II. Hatchability. *Farming in South Africa* 27, 408-410, 1952. 181
- SCHARRER, K. und W. SCHROPP, Fütterungsversuche mit Jod an Hühnern. *Die Tierernährung* 4, 249-264, 1932. 112

- SCHLOTTHAUER, C. F. and H. E. ESSEX, Observation on the fertility and hatchability of eggs from turkeys affected with enterohepatitis. *Cornell Veterinarian* 23, 81-82, 1933. 203
- SCHMALHAUSEN, L., Studien über Wachstum und Differenzierung. III. Die embryonale Wachstumskurve des Hühnchens. *Archiv für Entwicklungsmechanik* 108, 321-387, 1926. 200
- SCHMIDT, G., On the growth stimulating effect of eggwhite and its importance for the embryonic development. *Enzymologia* 1, 40-48, 1937. 90
- SCHUMACHER, A. E. and G. F. HEUSER, The importance of riboflavin in reproduction in poultry. *Poultry Science* (Abstract 17, 446, 1938) 18, 369-374, 1939a. 94
- SCHUMACHER, A. E. and G. F. HEUSER, Some properties of the new growth and reproduction factor with further results of its effect on chicks and hens. *Poultry Science* 18, 411-412, 1939b.
- SCHUMACHER, A. E. and G. F. HEUSER, Some properties of the alcohol-precipitate factor with further results of its effect on chicks and hens. *Poultry Science* 19, 315-320, 1940.
- SCHUMACHER, A. E., G. F. HEUSER and L. C. NORRIS, The complex nature of the alcohol precipitate factor required by the chick. *Journal of Biological Chemistry* 135, 313-320, 1940.
- SCHWANN, T., De necessitate aeris atmospherici ad evolutionem pulli in ovo incubito. Diss. Berlin, 1834. 65
- SCHWANN, T., Über die Nothwendigkeit der atmosphärischen Luft zur Entwicklung des Hühnchens in dem bebrüteten Ei. *Notizen aus dem Gebiete der Natur- und Heilkunde* 41, 241-245, 1834. 65
- SCHWARZ, L., Beobachtungen an Bruteiern, die vor der Bebrütung einige Zeit gelagert hatten. *Archiv für Geflügelkunde* 20, 405-420, 1956. 51
- SCHWARZ, L., Über Schädigungen von Bruteiern durch Erschütterungen vor und während der Bebrütung (11). *Deutsche Wirtschaftsgeflügelzucht* 11, 633-635, 1959. 54
- SCHWEIGERT, B. S., H. L. GERMAN, P. B. PEARSON and R. M. SHERWOOD, Effect of the pteroylglutamic acid intake on the performance of turkeys and chickens. *Journal of Nutrition* 35, 89-102, 1948. 99
- SCOTT, H. M., The effect of age and holding temperatures on hatchability of turkey and chicken eggs. *Poultry Science* 12, 49-54, 1933.
- SCOTT, H. M. and D. C. WARREN, Influence of ovulation rate on the tendency of the fowl to produce eggs in clutches. *Poultry Science* 15, 381-389, 1936. 74, 122, 124, 126
- SCOTT, H. M. and D. C. WARREN, The relation of total weight and the weight of component parts of the egg to hatching power. *Poultry Science* 20, 75-78, 1941. 69, 71, 72, 89
- SCOTT, J. P. and C. A. BRANDLY, Investigations of two outbreaks of laryngotracheitis. *Veterinary Alumni Quarterly* (Ohio State University) 22, 23-31, 1934. 202
- SECK, P., Der Einfluss heftiger Erschütterungen auf die Brutfähigkeit des Hühnereies. *Archiv für Geflügelkunde* 13, 362-367, 1939. 53, 54
- SECK, P., Die Innentemperatur des Hühnereies während der Brut. *Archiv für Kleintierzucht* 2, 212-225, 1941. 200
- SEREBROVSKY, A. S. and S. G. PETROFF, Downless chickens. *Journal of Heredity* 20, 331-332, 1929. 166
- SEREBROVSKY, R. E. and A. S. SEREBROVSKY, Studies on the genetics of the egg and egg laying. *Genetics of Domestic Fowl*, edited by N. K. Koltzoff. *Memoirs of Anikowo Genetical Station near Moscow. R.S.F.S.R. Commissariat of Agriculture. Moscow, 1926. Russian text pp. 102-121; English summary pp. 132-133. 85*

- SERGEEV, A. A. and S. S. KUDRIATSEV, Vliianie kormovykh faktorov na iatse-nockost' i inkubatsionnye kachestva iaits kur Belyi Leggorn (The influence of feed factors on the vitality and incubation qualities of eggs of White Leghorn hens). Sbornik Trudov Nauchno-Issledovatel'skii Institut Ptitsevodstva Narkomzema RSFSR (Publication of Scientific Research Institute for Poultry Breeding), Sel'khozgiz, 1941, pp. 87-105. 94, 108
- de SERRES, O., Le Théâtre d'Agriculture. Nouvelle édition. Paris (Madame Huzard), 1804-1805 (first edition: Paris, 1600). 26
- SHAKLEY, W. E. and C. W. KNOX, Hybridization of the pheasant and fowl. *Journal of Heredity* 45, 183-190, 1954 (Abstract: *Poultry Science* 32, 923, 1953). 167
- SHANNON, W. G. and M. P. DONNELLY, A further experiment on the effect of dry buffing on the hatchability of hen eggs. *Research and Experimental Record of the Ministry of Agriculture, Northern Ireland*, 1958, 8, 37-39, 1959. 55
- SHANNON, W. G. and E. C. KEENLEYSIDE, The effect of dry buffing on the hatchability of hen eggs. *Research and Experimental Record of the Ministry of Agriculture, Northern Ireland*, 1957, 7, 138-140, 1958. 55
- SHEARD, C. and G. M. HIGGINS, Influence of ultra-violet light, solar irradiation and cod-liver oil on production, fertility and incubation of eggs. *Proceedings of the Society for Experimental Biology and Medicine* 26, 615-618, 1928-1929. 105
- SHEARD, C. and G. M. HIGGINS, The influence of irradiation by air-cooled quartz-mercury arcs on the incubation of eggs. *Journal of Experimental Zoology* 57, 205-222, 1930. 105
- SHERWOOD, D. H., Effect of feeding methods on egg production, feed efficiency and hatchability with White Rock hens (Abstract). *Poultry Science* 36, 1157, 1957. 108
- SHERWOOD, D. H. and T. T. MILBY, Further tests with antibiotics for laying and breeding hens. *Poultry Science* 33, (Abstract 32, 932, 1952), 1031-1033, 1954. 101
- SHERWOOD, D. H., T. T. MILBY and W. A. HIGGINS, The effect of Nicarbazin on reproduction in White Rock breeder hens. *Poultry Science* 35, 1014-1019, 1956.
- SHERWOOD, D. H., T. T. MILBY and H. L. WITZ, Further studies on effect of Nicarbazin on reproduction of chickens (Abstract). *Poultry Science* 35, 1171, 1956. 136
- SHERWOOD, R. M., Vitamin A requirements of poultry. *Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939*, pp. 123-126.
- SHERWOOD, R. M. and G. S. FRAPS, The quantities of vitamin A required by pullets for maintenance and for egg production. *Texas Agricultural Experiment Station Bulletin* 468, 1932. 92
- SHERWOOD, R. M. and G. S. FRAPS, The amount of vitamin A potency required by hens for egg production. *Texas Agricultural Experiment Station Bulletin* 493, 1934. 92
- SHERWOOD, R. M. and G. S. FRAPS, The vitamin A requirements of hens for egg production. *Texas Agricultural Experiment Station Bulletin* 514, 1935. 93
- SHERWOOD, R. M. and G. S. FRAPS, Requirements of chickens for vitamin A when fed as carotene. *Texas Agricultural Experiment Station Bulletin* 583, 1940. 93
- SHIBATA, S. and A. MURATA, Studies on the hatching of the hen's egg. *Imperial Zootechnical Experiment Station, Chiba-Shi, Japan, Special Bulletin* 13, 1936. 68, 79
- SHOFFNER, R. N., The variation within an inbred line of S. C. W. Leghorns. *Poultry Science* 27, 235-236, 1948a. 175
- SHOFFNER, R. N., The reaction of the fowl to inbreeding. *Poultry Science* (Abstract 26, 555, 1947) 27, 448-452, 1948b. 175

- SHOFFNER, R. N., Performance of "incrosses" among lines of Leghorns. Abstract. Poultry Science 27, 683, 1948.
- SHOFFNER, R. N. and R. E. GRANT, Relaxed selection in a strain of White Leghorns. Poultry Science 39, 63-66, 1960. 175
- SHOFFNER, R. N. and H. J. SLOAN, Heritability studies in the domestic fowl. Official Report. Eighth World's Poultry Congress Copenhagen 1948, 1, 269-281, 1948. 183
- SHOFFNER, R. N., H. J. SLOAN, L. M. WINTERS, T. H. CANFIELD and A. M. PILKEY, Development and performance of inbred lines of chickens. Minnesota Agricultural Experiment Station Technical Bulletin 207, 1953. 175
- SHPITSER, S. M., Novoe y inkubatsii (News about incubation). Priroda (Moscow) 1948, No. 12, p. 87.
- SICARD, Réponse du Père Sicard, Missionnaire de la compagnie de Jésus en Égypte à un Mémoire de Messieurs de l'Académie des Sciences. Remarques sur les fous à poulets. Lettres édifiantes et curieuses, écrites des Missions Etrangères. Nouvelle édition. Mémoires du Levant 5, 432-441, Paris, 1780 (first edition: 7, 79, 1729). 19
- SIMON, R., Versuche über die Wirkung des Follikelhormons auf die Brut der Hühner. Diss. München, 1939. 107
- SINHA, M. D., R. K. RINGER, T. H. COLEMAN and H. C. ZINDEL, The effect of injected thiouracil on body weight and hatchability of the chick embryo. Poultry Science 38, 1405-1409, 1959. 113
- SIZEMORE, J. R., R. J. LILLIE, H. R. BIRD and C. A. DENTON, Further studies on the influence of aureomycin in the chick diet upon subsequent reproductive performance of laying hens. Poultry Science 34 (Abstract: 33, 1081, 1954), 432-435, 1955. 101
- SIZEMORE, J. R., R. J. LILLIE, C. A. DENTON and H. R. BIRD, Influence of aureomycin in the chick diet upon subsequent reproductive performance of laying hens. Poultry Science 32, (Abstract: 31, 935-936, 1952), 618-624, 1953. 101
- SJODIN, R. A., The behavior of brain and retinal tissue in mortality of the early chick embryo. Anatomical Record 127, 591-609, 1957. 130
- SKALLER, F., Heterosis from crisscross breeding in poultry. Report of Proceedings, Tenth World's Poultry Congress, Edinburgh, Scotland 13th-21st August, 1954, Part II, Section Papers, pp. 59-64, 1954. 175
- SKALLER, F., The Hagedoorn "nucleus system" of breeding—A critical evaluation based on an experiment with poultry. Proceedings of the Australian Society of Animal Production 1, 165-176, 1956. 175
- SKINNER, J. L., J. H. QUISENBERRY and J. R. COUCH, High efficiency and APF concentrates in the ration of the laying fowl. Poultry Science 30, 319-324, 1951. 100
- SKOGLUND, W. C., The relation between egg color and hatchability in meat type strains of New Hampshires. Delaware Agricultural Experiment Station Bulletin 281, 1950. 81
- SKOGLUND, W. C., The relationship between egg shape and hatchability in meat type strains of New Hampshires. Delaware Agricultural Experiment Station Bulletin 287, 1951. 74
- SKOGLUND, W. C. and A. W. BROWN, Effect of frequency of gathering eggs upon hatchability. Poultry Science 35, 369-371, 1956. 50
- SKOGLUND, W. C., A. E. TOMHAVE and A. F. KISH, Influence of management practices on the production of hatching eggs. Delaware Agricultural Experiment Station Bulletin 266, 1947.
- SKOGLUND, W. C., A. E. TOMHAVE and C. W. MUMFORD, The hatchability of eggs of various sizes. Poultry Science 27, 709-712, 1948. 72

- SKURATOV, I. S., (Lupine feed in fowl rations). *Nauka i Peredov. Opyt v S-kh Khoz* 1957, 31-32, 1957. Quoted from Biological Abstracts 35, 409, 1960. 169
- SMITH, A. H., U. K. ABBOTT and M. E. JONES, Effect of artificial changes in egg composition on hatchability and chick growth. *Proceedings of the Society for Experimental Biology and Medicine* 97, 17-20, 1958. 72, 89
- SMITH, G., Studies in the experimental analysis of sex. IX. On spermatogenesis and the formation of giant spermatozoa in hybrid pigeons. *Quarterly Journal of Microscopical Science* 58, 159-170, 1912-1913. 168
- SMITH, J. B., Malpositions—a factor in hatchability. *Proceedings of the Twenty-second Annual Meeting, Poultry Science Association* 1930, 1931, pp. 66-71. 190, 192
- SMITH, J. B., Some of the factors involved in embryonic mortality of the fowl. *Abstract. Poultry Science* 12, 320-321, 1933. 202
- SMITH, J. B., The sunshine factor in hatchability. *Atti del V. Congresso Mondiale di Pollicoltura tenutosi in Roma dal 6 al 15 Settembre 1933.* 2, 453-461, 1931. 108, 193
- SMITH, J. B. and H. D. BRANION, Hatchability studies with certain feeds. *Wissenschaftliche Berichte des VI. Weltgeflügelkongresses* 24. Juli bis 2. August 1936. Berlin und Leipzig 2, 77-83, 1936.
- SMITH, J. B. and H. D. BRANION, The influence of various forms of vitamin D on hatchability. *Poultry Science* 16, 367, 1937.
- SMITH, J. B. and H. D. BRANION, Influence of some protein supplements on hatchability. *Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A. July 28 to August 7, 1939, pp. 195-198.*
- SMITH, R. M., The influence of certain supplements on the production, hatchability, fertility and weight of eggs. *Arkansas Agricultural Experiment Station Bulletin* 293, 1933. 93
- SMITH, S. B., J. P. DELAPLANE and W. H. WILEY, The effect on production and hatchability of feeding laying pullets sulfaquinoxaline at the 0.033 percent level. *Poultry Science* 31, 679-680, 1952. 101
- SMYTH, JR., J. R., Hairy, a gene causing abnormal plumage in the turkey. *Journal of Heredity* 45, 197-200, 1954. 132
- SNELL, E. E. and W. W. CRAVENS, Reversal of aminopterin inhibition in the chick embryo with desoxyribosides. *Proceedings of the Society for Experimental Biology and Medicine* 74, 87-91, 1950. 99
- SNYDER, E. S., Some observations made in connection with the study of the inheritance of hatching power in Barred Plymouth Rocks. *Proceedings of the Twenty-second Annual Meeting, Poultry Science Association, Macdonald College, Quebec, Canada, July 9-11, 1930, pp. 60-64.* 182
- SPRAT, T., The History of the Royal-Society of London, for the Improving of Natural Knowledge. London (J. Martyn), 1667. 32
- STADELMAN, W. J., The effects of sound of varying intensity on hatchability of chicken egg. *Poultry Science* 37, 166-169, 1958. 65
- STEELE, D. G. and W. M. INSKO, JR., Embryonic position in relation to age of hen. *Official Report, Eighth World's Poultry Congress Copenhagen 1948, I, 331-335, 1948.* 192
- STEFANI, F., Ricerche sull' azione di estratti di prostate e di altre ghiandole sullo sviluppo delle uova e del pulcino di pollo. *Archivio di Fisiologia* 36, 370-404, 1936. 107
- STEINER, H., Über letale Fehlentwicklung der zweiten Nachkommenschafts - Generation bei tierischen Artbastarden. *Archiv der Julius Klaus - Stiftung für Vererbungs-forschung, Sozialanthropologie und Rassenhygiene* 20, Ergänzungsband, 236-251, 1945. 168

- STEPHENSON, A. B., Supplemental oxygen for high altitude incubation. Abstract. Poultry Science 29, 781, 1950. 61
- STEPHENSON, E. L. and B. B. CLOWER, The influence of an unidentified factor found in fish solubles on hatchability (Abstract). Poultry Science 31, 936-937, 1952.
- STEPHENSON, E. L., C. DICKSON and B. D. BARNETTE, An unidentified forage juice factor necessary for optimum reproduction in White Wyandotte hens (Abstract). Poultry Science 33, 1083, 1954.
- STERN, B. J., Resistance to the adoption of technological innovations. In: Technological Trends and National Policy, Including the Social Implications of New Inventions. Report of the Subcommittee on Technology to the National Resources Committee. Washington (U.S. Government Printing Office), 1937. 46
- STEWART, G. F., Shell characteristics and weight losses of hen's eggs. Ph.D. Thesis, Cornell University (Ithaca, N.Y.), 1933. 85
- STEWART, J. H. and H. ATWOOD, Poultry experiments. West Virginia Agricultural Experiment Station Bulletin 71, 1900.
- STEWART, J. H. and H. ATWOOD, Poultry experiments. West Virginia Agricultural Experiment Station Bulletin 86, 1903.
- STEWART, J. H. and H. ATWOOD, Some factors influencing the vigor of incubator chickens. West Virginia Agricultural Experiment Station Bulletin 124, 1909. 57
- STILES, K. A. and R. L. WATTERSON, The effect of jarring upon the embryogeny of chick embryos. Anatomical Record 70, 7-12, 1937-1938. 64
- STILWELL, E. F., The influence of temperature variation upon the occurrence of multipolar mitoses in embryonic cells grown in vitro. Anatomical Record 99, 227-238, 1947. 190
- STODDARD, H. H., Incubation: Natural and Artificial. Hartford, 1886. 46
- STRESEMANN, E., Aves. Kückenthal-Krumbach, Handbuch der Zoologie 7, 2, Berlin und Leipzig 1927-1934. 5, 8
- STRONG, R. M., A Bibliography of Birds. Field Museum of Natural History, Zoological Series 25, 1939.
- STUART, H. O. and C. P. HART, The effect of different calcium intake on egg production, shell strength and hatchability. Poultry Science 17, 3-7, 1938. 88
- STURKIE, P. D., A new type of nakedness in the domestic fowl. Poultry Science 20, 474, 1941. 166
- STURKIE, P. D., A new type of autosomal nakedness in the domestic fowl. Journal of Heredity 33, 202-208, 1942. 166
- STURKIE, P. D. and A. G. WILLIAMS, Studies on pregastrular development, early embryonic development, and hatchability of prematurely laid eggs of the hen. Poultry Science 24, 546-554, 1945.
- SUNDE, M. L. and H. R. BIRD, The effect of pullet maturity on fertility and hatchability of eggs. Poultry Science (Abstract: 36, 1161, 1957) 38, 272-279, 1959. 116
- SUNDE, M. L., W. W. CRAVENS, H. W. BRUNS, C. A. ELVEHJEM and J. G. HALPIN, The pteroylglutamic acid requirement of laying and breeding hens. Poultry Science 29, 220-226, 1950. 99
- SUNDE, M. L., W. W. CRAVENS, C. A. ELVEHJEM and J. G. HALPIN, The effect of diet and cecectomy on the intestinal synthesis of biotin in mature fowl. Poultry Science 29, 10-14, 1950a.
- SUNDE, M. L., W. W. CRAVENS, C. A. ELVEHJEM and J. G. HALPIN, The effect of folic acid on embryonic development of the domestic fowl. Poultry Science 29, 696-702 (Abstract p. 781-782), 1950b. 99

- SUNDE, M. L., J. G. HALPIN and W. W. CRAVENS, The effect of vitamin B₁₂ supplements and antibiotic feed supplements on egg production and hatchability. *Poultry Science* 31, 617-620, 1952. 100
- SUSCIKA, A., Ivaros hibridizálási kísérletek baromfifajok között (Experiments on interspecific hybridization of poultry). *Agrártudományi Egyetem Allattenyésztési Karának Közleményei, Gödöllő-Budapest* 2, 103-109, 1956. 167
- SVENSSON, S. A., Der Einfluss der Beschaffenheit der Eierschale auf die Brutfähigkeit von Hühnereiern. *Archiv für Geflügelkunde* 21, 145-158, 1957. 87
- SZEPSENWOL, J., Recherches sur les centres organisateurs des vésicules auditives chez des embryons de poulets omphalocéphales obtenus expérimentalement. *Archives d'Anatomie Microscopique* 29, 5-94, 1933. 196
- SZEPSENWOL, J., Les conditions embryologiques qui mènent à la formation d'un cœur unique ou double, ainsi que celles qui causent l'asymétrie normale ou inverse de l'organe pulsatile chez des embryons de Poulet omphalocéphales produits expérimentalement. *Archives d'Anatomie, d'Histologie et d'Embryologie* 17, 307-370, 1934. 196
- TALMADGE, D. W., The effect of diethylstilbestrol implantation in eight-week pullets on their reproductive ability. *Poultry Science* 38, 211-213, 1959. 107
- TARNAVSKY, N., The effect of x-rays on the embryonic development of hens' eggs. Academy of Sciences of the Ukrainian SSR. Institute of Zoology and Biology. *Memoirs on Genetics* No. 2, 91-107, 1938. 196
- TAYLOR, A., J. THACKER and D. PENNINGTON, The effect of increased pantothenic acid in the egg on the development of the chick embryo. *Science* 94, 542-543, 1941. 97
- TAYLOR, L. W., Early orientation of the chick embryo in relation to malposition and hatchability. *Poultry Science* 11, 368, 1932. 191
- TAYLOR, L. W., Heterotaxia in chick embryos. *Poultry Science* 13, 378, 1934. 191
- TAYLOR, L. W., The effect of folic acid on egg production and hatchability. *Poultry Science* (Abstract 25, 412-413, 1946) 26, 372-376, 1947. 99
- TAYLOR, L. W., U. K. ABBOTT and C. A. GUNNS, Further studies on diplopodia. I. Modification of phenotypic segregation ratios by selection. *Journal of Genetics* 56, 161-178, 1959. 156
- TAYLOR, L. W. and C. A. GUNNS, Size of unincubated embryo in relation to hatchability. Abstract. *Poultry Science* 14, 294, 1935. 184
- TAYLOR, L. W. and C. A. GUNNS, Development of the unincubated chick embryo in relation to hatchability of the egg. *Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939*, pp. 188-190. 184
- TAYLOR, L. W. and C. A. GUNNS, Diplopodia: a lethal form of polydactyly in chickens. *Journal of Heredity* 38, 67-76, 1947. 154-157
- TAYLOR, L. W., C. A. GUNNS, C. R. GRAU and S. LEPKOVSKY, Effect of a respiratory disease on reproduction. *Poultry Science* 32, 129-137, 1953. 202
- TAYLOR, L. W., C. A. GUNNS and B. D. MOSES, The effect of current interruption in electrical incubation. *California Agricultural Experiment Station Bulletin* 550, 1933. 56
- TAYLOR, L. W. and I. M. LERNER, Inheritance of eggshell thickness in White Leghorn pullets. *Journal of Agricultural Research* 58, 383-396, 1939. 141
- TAYLOR, L. W., D. C. LOWRY and E. G. RAGGI, Effects of an outbreak of avian encephalomyelitis (epidemic tremor) in a breeding flock. *Poultry Science* 34, 1036-1045, 1955. 203

- TAYLOR, L. W., R. A. SJODIN and C. A. GUNNS. The gaseous environment of the chick embryo in relation to its development and hatchability. 1. Effect of carbon dioxide and oxygen levels during the first four days of incubation upon hatchability. *Poultry Science* 35, (Abstract 32, 926-927, 1953), 1206-1215, 1956. 66
- TAYLOR, M. W., J. R. STERN, W. C. RUSSELL and E. JUNGHERR. The pro-vitamin A requirement of hens. *Poultry Science* 26, 243-254, 1947. 94
- TAZELAAR, M. A., The effect of a temperature gradient on the early development of the chick. *Quarterly Journal of Microscopical Science* 72, 419-446, 1928. 196
- TEEKELL, R. A. and A. B. WATTS, Tungsten supplementation of breeder hens. *Poultry Science* 38, 791-794, 1959.
- TEMPERTON, H. and F. J. DUDLEY, The effects of progressive vitamin-A depletion in adult fowls as indicated by economic characteristics, liver storage and clinical symptoms of avitaminosis. *Harper Adams Utility Poultry Journal* 31, N.S. No. 4, 61-77, 1946. 93
- TEMPERTON, H. and F. J. DUDLEY, The effects of using preformed vitamin A as the sole dietary source of vitamin A for growing chickens and adult fowls. *Harper Adams Utility Poultry Journal* 32, N.S. No. 4, 1-28, 1947. 93
- TEMPERTON, H. and F. J. DUDLEY, Vitamin-A metabolism in poultry. *Harper Adams Utility Poultry Journal* 33, N.S. No. 4, 1-36, 1948. 93
- THEVENOT, Voyages de Mr. de Thévenot en Europe, Asie & Afrique. 3ème édition. Amsterdam (M. C. Le Cène), 1727 (first published in 1674). 19
- THOM, C. C., Carbon dioxide in relation to incubation. *Ontario Agricultural College Bulletin* 163, 51-56, 1908. 65
- THOMPSON, R. L., Incubation at high altitudes. The effects of wind, barometric pressure and humidity on foetal mortality in the hen's egg. *Poultry Science* 31, 497-509, 1952. 61
- THORNDIKE, L., A History of Magic and Experimental Science during the First Thirteen Centuries of our Era I, New York (Macmillan Co.), 1929. 24, 25
- THORNTON, E. J., Possible genetic factors and embryonic mortality in relation to the sex ratio of chicks at hatching. Thesis, Massachusetts State College, 1944. 170
- THORNTON, P. A. and R. E. MORENG, Egg production and reproduction as affected by arsenic acid and penicillin. *Poultry Science* 37, 551-557, 1958. 101
- van TIENHOVEN, A., R. D. CRAWFORD and S. A. DUCHAINE, The effect of Nicarbazine on spermatogenesis and semen quality. *Poultry Science* 36, 760-762, 1957. 136
- TIERIE, G., Cornelis Drebbel (1572-1633). Proefschrift, Leiden, 1932. 28
- TIRELLI, V., Sull'influenza delle basse temperature sull'evoluzione dell'embrione di pollo. *Annali di Freniatria* 9, 149-173, 1899. 55
- TIRELLI, V., De l'influence des basses températures sur l'évolution de l'embryon de poulet. *Archives Italiennes de Biologie* 33, 37-50, 1900. 55
- TITTELER, R. P., B. W. HEYWANG and T. B. CHARLES, The occurrence and significance of *Salmonella pullorum* in eggs. *Pennsylvania Agricultural Experiment Station Bulletin* 235, 1928.
- TITUS, H. W., Nutritional factors in relation to hatchability. Proceedings. Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939, pp. 198-201.
- TITUS, H. W., Practical nutritive requirements of poultry. Food and Life. Year-book of Agriculture. U.S. Department of Agriculture 1939, pp. 787-818.
- TITUS, H. W., Variation of egg production and hatchability. *Poultry Science* 32, 593-601, 1953. 9

- TITUS, H. W., T. C. BYERLY, N. R. ELLIS and R. B. NESTLER, Effect of packing-house byproducts in the diet of chickens, on the production and hatchability of eggs. *Journal of Agricultural Research* 53, 453-465, 1936. 108
- TITUS, H. W., T. C. BYERLY, N. R. ELLIS and R. B. NESTLER, Effect of the calcium and phosphorus content of the diet of chickens on egg production and hatchability. *Poultry Science* 16, 118-128, 1937. 111
- TITUS, H. W. and R. B. NESTLER, Effect of vitamin D on production and some properties of eggs. *Poultry Science* 14, 90-98, 1935. 105
- TOMHAVE, A. E., Influence of age of New Hampshire female breeders upon hatchability of eggs. *Poultry Science* 35, 236-237, 1956. 116, 119
- TOMHAVE, A. E., Fertility and hatchability of eggs produced by New Hampshire breeders during their first 365 days of production. *Poultry Science* 37, 27-29, 1958. 119
- TOMLINSON, H., Artificial Incubation and the Breeding and Rearing of Poultry, for Market and Exhibition. London (Simpkin, Marshall and Co.), 1880. 44
- TORR, C., Rhodes in Modern Times. Cambridge (University Press), 1887. 8
- TOUCHBURN, S. P., J. BIELY and B. MARCH, The effect of dehydrated green feed on fertility and hatchability of eggs from three generations of New Hampshire chickens. *Poultry Science* 36, (Abstract 35, 1177-1178, 1956), 591-595, 1957.
- TOURTECHOT-GRANGER, Relation d'un voyage fait en Égypte par le sieur Granger en 1730, où l'on voit ce qu'il y a de plus remarquable, particulièrement sur l'histoire naturelle. Paris, 1745 (English translation: London, 1773). 19
- TOWNSLEY, T. S., Humidity in incubation. Proceedings of Twenty-first Annual Meeting, Poultry Science Association, 1929. Bulletin of Alabama Polytechnic Institute 25, 56-60, 1930. 60
- TOWNSLEY, T. S., The humidity factor in incubation. Report of Proceedings of the 4th World's Poultry Congress at the Crystal Palace, London, England: July 22-30, 1930, 136-145, 1931. 59, 60
- TRETIKOV, N. P., Usushka iaits, embrionalnyi rost, smertnost' i vyvodnost' pri estestvennoi inkubatsii v sravnenii s iskusstvennoi (Loss of water, embryonic growth, mortality and hatchability in natural as compared with artificial incubation). Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936, pp. 30-32.
- TRETYAKOV, N. P., Natural and artificial incubation. Problemy Zhivotnovodstva (Problems of Animal Husbandry) 1937, No. 1, pp. 84-101. 5
- TRETIKOV, N. P., Inkubatsiia. 2nd edition. Moscow, 1953. 57
- TRETIKOV, N. P., Vliianie peremennykh temperatur na razvitie ptits (The effect of varying temperatures on the development of birds). Trudy Nauchno Issledovatel'skogo Instituta Ptitsevodstva 24, Inkubatsiya, 5-12, 1954. 57
- TRETIKOV, N. P. and S. O. PEL'TTSEER, Prakticheskoe primeneniye novogo metoda othora iaits dlia inkubatsii posle predvaritelnogo ikh progrevaniia (The practical application of a new method of selecting eggs for incubation after preliminary warming). Trudy Nauchno-Issledovatel'skogo Instituta Ptitsevodstva 24, Inkubatsiya, 176-184, 1954. 186
- TRETIKOVA, E. L., Vliianie na protsess razvitiia i rezultaty inkubatsii iaits kur izmenenii rezhima inkubirovaniia pod vlianiem izmenenii vlazhnosti. IV. Fiziko-khimicheskie izmeneniia plazm iaits. (The effect of changes in humidity on the processes of development and the results of incubation of chicken eggs. IV. Physico-chemical changes in albumen and yolk). Sbornik referatov Nauchno-Issledovatel'skikh rabot NIIP 1936, pp. 27-29.
- TRETIKOVA, E. L., Vliianie vlazhnosti na fiziko-khimicheskie izmeneniia plazm iaitsa (Influence of humidity on the physico-chemical changes of the egg plasma). Sbornik Trudov Nauchno-Issledovatel'skii Institut Ptitsevodstva Narkomzema RSFSR (Publication of Scientific Research Institute for Poultry Breeding), Sel'khozgiz, 1941, pp. 224-232. 62

- TRETYAKOV, N. P., (Incubation of eggs and rearing of the young stock of farm poultry) Tr. Inst. Morfol. Zhivot. Akad. Nauk SSSR 1957, pp. 249-252 (Quoted from Biol. Abstr. 35, 4154, 1960).
- TUR, J., Sur une série d'embryons monstrueux provenant de poules primipares. Bulletin de la Société Philomatique de Paris 9ème série 9, 78-100, 1907. 116
- TYLER, C., The porosity of egg shells, and the influence of different levels of dietary calcium upon porosity. Journal of Agricultural Research 35, 168-176, 1945. 88, 186
- UBBELS, P., Broederyproeven op het Ryksinstituut voor Pluimveeteelt te Beekbergen. 1953. 63
- UMANSKI, E., Zur Frage über den Einfluss der vertikalen Lage des Eies auf die Entwicklung von Gallus domesticus, Zoologischer Anzeiger 68, 81-87, 1926.
- UPP, C. W., Studies on embryonic lethal characters in the domestic fowl. Louisiana Agricultural Experiment Station Bulletin 255, 1934. 142, 192, 194
- UPP, C. W. and R. B. THOMPSON, Influence of time of hatch on hatchability of the eggs, rate of growth of the chicks, and characteristics of the adult female. Oklahoma Agricultural Experiment Station Bulletin 167, 1927.
- UPP, C. W. and N. F. WATERS, A sex-linked lethal gene in the single comb White Leghorn fowl. Poultry Science 14, 372 and 379, 1935. 142
- della VALLE, P., Viaggi di Pietro della Valle il Pellegrino, con minuto ragguaglio di tutte le cose notabili osservate in essi, descritti da lui medesimo in 54. Lettere familiari, Da diversi luoghi della intrapresa pellegrinatione. Mandate in Napoli all'erudito, e fra' piu cari, di molti anni suo Amico. Mario Schipano. Divisi in tre Parti. Cioe, La Tyrchia, La Persia e L'India. Bologna (Angelo Maria Angelelli). 1672. (First edition Rome 1650/53). 19
- VALLEE, A., Cinq lettres inédites de Jean François Gaultier à M. de Rhéaumur de l'Académie des Sciences. Proceedings and Transactions of the Royal Society of Canada 3rd series 24, section I, 31-43, 1930. 39
- VECCHI, A., Osservazioni sugli effetti della consanguinità nella selezione dei polli. Wissenschaftliche Berichte des VI. Weltgeflügelkongresses 24. Juli bis 2. August 1936. Berlin und Leipzig, 2, 86-89, 1936. 174
- VESLING, Joannis Veslingi Mindani Equitis Observationes Anatomicae et Epistolae Medicae ex schedis posthumis selectae et editae à Th. Bartholino. Hafniae, 1664. 19
- VEYRE, A., Quelques mots sur l'incubation artificielle. Revue Française d'Ornithologie Scientifique et Pratique 6, année 11, 69-70, 1920.
- VEZZANI, V. and R. QUILICI, Researches about the influence of various factors on the hatchability in White Leghorns, Rhode Island Reds and New Hampshires bred in "Piemonte". Official Reports IXth World's Poultry Congress Paris 1951, 1, 114-117.
- VICKERS, G. S., A hatchability study among Ohio hatcheries. Poultry Science 15, 496-500, 1936. 133
- de la VIGNE, A., Le Vergier d'Honneur. Archives curieuses de l'histoire de France depuis Louis XI jusqu'à Louis XVIII, par L. Cimber. 1re série, 1, 315-435, Paris, 1834 (first written and printed soon after 1495). 21
- da VINCI, LEONARDO, The Notebooks of Leonardo da Vinci arranged, rendered into English and introduced by Edward MacCurdy. 2 vols. New York (Reynal & Hitchcock), 1923. 26
- VISSCHEDIJK, A. H. J. and J. W. KUIPER, Über die Fehllage des Hühnerembryos im Ei. Archiv für Geflügelkunde 19, 73-86, 1955.
- VLADIMIROVA, IU. N., Poteria v vese laits pered inkubatsii (Loss in weight of eggs prior to incubation). Trudi Nauchno-Issledovatel'skogo Instituta Ptitsyovodstva, 24, Inkubatsiya, 126-155, 1954. 81, 82
- VOITELLIER, L'incubation artificielle et la basse-cour. Paris (A. Chaix et Cie.), 1878.

- VOITELLIER, L'incubation artificielle et la basse-cour. 2nd ed. Mantes (Beaumont Frères), 1880. 44
- VOITELLIER, C., Comment devrait être appréciée la faculté d'éclosion des oeufs. *Wissenschaftliche Berichte des VI. Weltgeflügelkongresses* 24. Juli bis. 2. August 1936, Berlin und Leipzig, 2, 89-90, 1936. 75, 79, 90
- VAN WAGENEN, A., Interior egg quality factors, their changes and inheritance behavior. Ph.D. Thesis, Cornell University, Ithaca, N.Y., 1935. 90
- VAN WAGENEN, A. and G. O. HALL, The inheritance of certain characters affecting egg quality. *Poultry Science* 15, 405-410, 1936. 90
- WAGLEY, P. F. and H. R. MORGAN, Effects of folic acid antagonists inoculated in embryonated eggs. *Archives of Pathology* 46, 441-450, 1948. 99
- WAIBEL, P. E., M. L. SUNDE and W. W. CRAVENS, Effect of addition of penicillin to the hen's ration on biotin and folic acid content of eggs. *Poultry Science* 31, 621-624, 1952. 101
- WAITE, R. H., The effect of age of eggs on their hatching quality. *Maryland Agricultural Experiment Station Bulletin* 233, 1919. 49, 53
- WAITE, R. H., The effect of age of eggs on their hatching quality. *Utility Poultry Journal* 9, 70-75, 1923-1924. 49
- WALKER, A. L. and G. E. VOSS, Artificial incubation of hen eggs in New Mexico. *New Mexico Agricultural Experiment Station Bulletin* 147, 1925.
- WALTHER, Artificial incubation: being the practical account of the art and science of Mr. Walther, for hatching of all kinds of poultry and game birds by steam: with the proved method of fostering and rearing without the aid or care of a parent-bird. London, 1824. 43
- WANG, CHUAN-YI, Chinese artificial hatching method. K'ang method. North Tungchow method. (In Chinese). Peiping (Ta-Hwa Publishing Co.), 1938. 16
- WARREN, D. C., Hybrid vigor in poultry. *Poultry Science* 7, 1-8, 1927-1928. 174
- WARREN, D. C., Non-heritable downlessness in chickens. *Journal of Heredity* 21, 408, 1930. 166
- WARREN, D. C., Inheritance of albinism in the domestic fowl. *Journal of Heredity* 24, 379-383, 1932. 138
- WARREN, D. C., The influence of some factors on the hatchability of the hen's egg. *Kansas Agricultural Experiment Station Technical Bulletin* 37, 1934. 69, 70, 115, 117, 133, 134, 174
- WARREN, D. C., The lethal nature of flightlessness in the fowl. *Journal of Heredity* 28, 16-18, 1937. 167
- WARREN, D. C., The crossbreeding of poultry. *Kansas Agricultural Experiment Station Technical Bulletin* 52, 1942. 178
- WARREN, D. C. and L. KILPATRICK, Fertilization in the domestic fowl. *Poultry Science* 8, 237-256, 1928-1929. 128
- WARREN, D. C. and H. M. SCOTT, An attempt to produce turkey-chicken hybrids. *Journal of Heredity* 26, 104-107, 1935. 167
- WATERS, N. F., Inbreeding in White Leghorn fowls. *Proceedings of the Sixth International Congress of Genetics*, Ithaca, N.Y., 1932, 2, 205-206. 176
- WATERS, N. F., Certain so-called malpositions a natural occurrence in the normal development of the chick embryo. *Poultry Science* 14, 208-216, 1935a. 192
- WATERS, N. F., Changes in the position of chick embryos after the eighteenth day of incubation. *Science* 82, 66-67, 1935b. 192

- WATERS, N. F., The influence of inbred sires top-crossed on White Leghorn fowl. *Poultry Science* 17, 490-497, 1938. 176
- WATERS, N. F., The hatchability of chicken eggs as influenced by diallel crossing. *Poultry Science* 23, 495-496, 1944. 181
- WATERS, N. F., The influence of inbreeding on hatchability. *Poultry Science* 24, 329-334, 1945. 143, 176
- WATERS, N. F. and J. H. BYWATERS, A lethal embryonic wing mutation in the domestic fowl. Abstract. *Poultry Science* 20, 477, 1941. 150
- WATERS, N. F. and J. H. BYWATERS, A lethal embryonic wing mutation in the domestic fowl. *Journal of Heredity* 34, 213-217, 1943. 150
- WATERS, N. F. and W. V. LAMBERT, Inbreeding in the White Leghorn fowl. Iowa Agricultural Experiment Station Research Bulletin 202, 1936a. 176-178
- WATERS, N. F. and W. V. LAMBERT, A ten year inbreeding experiment in the domestic fowl. *Poultry Science* 15, 207-218, 1936b. 176
- WATSON, O. M., Artificial incubation of chickens. South Carolina Agricultural Experiment Station Bulletin 81, 1903.
- WELCH, B. E., R. W. PERRETT, J. H. CLEMENTS and J. R. COUCH, The relation of vitamin B₁₂ to egg yolk storage of folic acid. *Journal of Nutrition* 54, 601-608, 1954. 101
- WESSELKIN, N., Über den Einfluss des Sauerstoffmangels auf das Wachstum und die Entwicklung von Hühnerembryonen. *Zentralblatt für Allgemeine Pathologie und Pathologische Anatomie* 24, 1033-1034, 1913. 65
- WEST, H. O., A compilation of experimental information on feeding laying hens. Mississippi Agricultural Experiment Station Bulletin 330, 1939.
- WESTERMAYER, H., Bessere Schlupfergebnisse durch Verfütterung von Geschlechtshormonen an die Zuchttiere. *Deutsche landwirtschaftliche Geflügelzeitung* 39, 283, 1936. 107
- WESTFALL, B. A., Comparative toxicity of selenium in the presence of various sulfur compounds. Thesis, Graduate School, University of Missouri, 1938. University Microfilms, Ann Arbor, Michigan, Publication No. 97. 113
- WHEELER, S. R. and E. HOFFMANN, Influence of quantitative thyroprotein treatment of hens on length of incubation period and thyroid size of chicks. *Endocrinology* 43, 430-439, 1948. 112
- WHITSON, D., H. W. TITUS and H. R. BIRD, Effect of dietary level of soybean meal on hatchability. *Poultry Science* 25, 52-58, 1946a. 110
- WHITSON, D., H. W. TITUS and H. R. BIRD, The effect of feeding cow manure on egg production and hatchability. *Poultry Science* 25, 143-147, 1946b. 110
- WILGUS, JR., H. S. and F. X. GASSNER, Effect of soybean oil meal on avian reproduction. *Proceedings of the Society for Experimental Biology and Medicine* 46, 290-293, 1941. 109
- WILGUS, H. S. JR., F. X. GASSNER, A. R. PATTON and G. S. HARSHFIELD, The iodine requirements of chickens. Colorado Agricultural Experiment Station Technical Bulletin 49, 1953 (Abstract: *Poultry Science* 27, 686, 1948). 112
- WILGUS, H. S., L. C. NORRIS and G. F. HEUSER, The role of manganese in poultry nutrition. *Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939*, pp. 171-174. 111
- WILGUS, H. S. and W. W. SADLER, Incubation factors affecting hatchability of poultry eggs. I. Levels of oxygen and carbon dioxide at high altitudes. *Poultry Science* 33, 460-471, 1954. 62
- WILGUS, JR., H. S. and D. V. ZANDER, Minimum levels of animal protein for reproduction. *Poultry Science* 23, 344-346, 1944. 109

- WILHELM, L. A., Effect of interior quality of eggs on their hatchability. Proceedings, Seventh World's Poultry Congress and Exposition, Cleveland, Ohio, U.S.A., July 28 to August 7, 1939, pp. 191-194. 71, 75, 90
- WILKINSON, J. G., Topography of Thebes, and General View of Egypt. London (John Murray), 1835. 19
- WILLIAMS, J. K., C. E. LAMPMAN and D. W. BOLIN, The efficiency of carotene as supplied by alfalfa meal in meeting the vitamin A requirements of laying hens. Poultry Science 18, 268-275, 1939. 93
- WILSON, C. W., Some effects of the gamma rays of radium on the developing chick embryo. Acta Radiologica 16, 719-734, 1935. 196
- WILSON, W. O., Viability of embryos and of chicks in inbred chickens. Poultry Science 27, 727-735, 1948. 175, 183
- WOLFF, C., Vernünftige Gedancken von den Würckungen der Natur/Den Liebhabern der Wahrheit mitgetheilet von Christian Wolff. 2nd ed. Halle im Magdeburg (Rengerische Buchhandlung), 1725. (First edition 1723). 75
- WOLFF, C., Vernünftige Gedancken von den Absichten der natürlichen Dinge. 3rd ed. Franckfurt und Leipzig (Rengerische Buchhandlung), 1737. (First edition 1724). 75
- WOLFF, E., Recherches sur la structure d'omphalocéphales obtenus expérimentalement. Archives d'Anatomie, d'Histologie et d'Embryologie 16, 135-193, 1933. 196
- WOLFF, E., Recherches expérimentales sur la cyclopie. Archives d'Anatomie, d'Histologie et d'Embryologie 18, 145-168, 1934. 196
- WOLFF, E., Recherches expérimentales sur l'otocéphalie et les malformations fondamentales de la face. Archives d'Anatomie, d'Histologie et d'Embryologie 18, 229-262, 1934. 196
- WOLFF, E., Les bases de la tératogénèse expérimentale des vertébrés amniotes, d'après les résultats de méthodes directs. Archives d'Anatomie, d'Histologie et d'Embryologie 22, 1-382, 1936. 196
- WOLFF, E., La science des monstres. Paris (Librairie Gallimard), 1948. 196
- W. I. GENT, (WORLIDGE, J.), Systema Agriculturae; the Mystery of Husbandry Discovered, 4th edition. London, 1697 (first edition 1669). 36
- WORM, O., Olai Wormii ed ad eum Doctorum virorum Epistolae, medici, anatomici, botanici, physici & historici argumenti: rem vero literariam, linguasque & antiquitates Boreales potissimum illustrantes. Havniae, 1751. 22
- van der WOUDE, C., Kronych van Alckmaar. 's Gravenhage, 1746 (first edition: Amsterdam and Alckmaar, 1743). 29
- WRIGHT, L., The Illustrated Book of Poultry. London (Cassel & Company), 1890. 46
- WYATT, A. J., Combining ability of inbred lines of Leghorns. Poultry Science 32, 400-405, 1953. 175
- YACOWITZ, H., R. F. MILLER, L. C. NORRIS and G. F. HEUSER, Vitamin B₁₂ studies with the hen. Poultry Science 31, 89-94, 1952. 101
- YAMASHINA, Y., On the hybrid between the domestic fowl and the common pheasant. Japanese Journal of Genetics 18, 231-253, 1942. 167
- YANG, HSIN, Pin-feng kuang-i. (Chinese original in Library of Congress. Reprinted in: Nung-hsüeh ts' ung-shu. Shanghai nung-hsüeh hui. Shanghai, about 1900. The Gest Oriental Library, Catalogue No. 1668, series I. vol. 15). 10, 16, 24
- YATES, J. D. and P. J. SCHAIBLE, Zinc supplementation on hen rations containing different levels of calcium (Abstract). Poultry Science 39, 1307/8, 1960. 111

- YESAIR, D. W., D. E. McOSKER and L. J. DANIEL. The effect of vitamin B₁₂ on the synthesis of phospholipides and sphingosine in the developing chick embryo. *Archives of Biochemistry and Biophysics* 79, 168-176, 1959. 101
- YOUNGNER, J. S., E. N. WARD and J. E. SALK. Effect of 5-amino-7-hydroxy-1-H-v-triazole(d) pyrimidine on growth and development of the chick embryo. *Proceedings of the Society for Experimental Biology and Medicine* 75, 157-161, 1950. 110
- ZAJTAY, (ZAITSCHEK), A., Über die Wirkung der Beifütterung kleiner Jodmengen auf den Eierertrag von Hühnern und auf das Schlüpfergebnis. *Die Tierernährung* 6, 102-111, 1934. 112
- ZNOJLOVÁ, V., V. ZOUFALÝ and V. PATKOVÁ. Návrh na zlepšení síly vaječné skořápky v plemenných chovech drůbeže. A proposition for shell strength improvement in the breed flock of poultry. *Sborník Československé Akademie Zemědělských Věd Živočišná Výroba* 4, 553-562, 1959. 75
- ZWILLING, E., Association of hypoglycemia and insulin micromelia in chick embryos. *Journal of Experimental Zoology* 109, 197-214, 1948. 194
- ZWILLING, E., The role of epithelial components in the developmental origin of the "wingless" syndrome of chick embryos. *Journal of Experimental Zoology* 111, 175-188, 1949a. 151
- ZWILLING, E., Reversal of insulin-induced hypoglycemia in chick embryos by nicotinamide and α -ketoglutaric acid. *Proceedings of the Society for Experimental Biology and Medicine* 71, 609-612, 1949b. 194
- ZWILLING, E., Interaction between limb bud ectoderm and mesoderm in the chick embryo. IV. Experiments with a wingless mutant. *Journal of Experimental Zoology* 132, 241-251, 1956. 151
- ZWILLING, E. and J. T. DeBELL, Micromelia and growth retardation as independent effects of sulfanilamide in chick embryos. *Journal of Experimental Zoology* 115, 59-81, 1950. 194

ADDENDA TO LITERATURE

Received too late for discussion in text

- ABBOTT, U. K., L. W. TAYLOR and H. ABLANALP, Studies with talpid², an embryonic lethal of the fowl. *Journal of Heredity* 51, 194-202, 1960.
- ARIYAMA, H. and S. KIMURA, Studies on pantothenic acid antagonists. *Journal of Vitaminology* 6, 52-61, 1960.
- COLES, R., The influence of housing systems and aging of layers on egg quality and hatching. *Poultry Science* 39, 1365-1376, 1960.
- COOPER, D., B. MARCH and J. BIELY, The performance of laying pullets fed rations differing in cereal component and protein supplement. *Poultry Science* 39, 1395-1400, 1960.
- DOBRYNINA, A. JA, I. G. KOSTIN, L. A. ZUBAREVA, A. I. SAMOLETOV and M. G. SALGANNIK, Vlijanie mikrodoz ionizirujuščih izlučenii na ontogenez sel'skokochozjaistvennyh ptic (The effect of microdoses of ionising radiation on the growth of domestic poultry). *Zivotnovodstvo* 22, 61-65, 1960. Quoted from *Animal Breeding Abstracts* 18, 456, 1960.
- FUNK, E. M. and J. E. FORWARD, Effect of pre-incubation on the hatchability of chicken eggs. *Missouri Agricultural Experiment Station Research Bulletin* 695, 1960.
- FUNK, E. M. and J. E. FORWARD, Effect of holding temperature on hatchability of chicken eggs. *Missouri Agricultural Experiment Station Research Bulletin* 732, 1960.

- GEISSLER, B., Untersuchungen über die künstliche Brut zur Verbesserung der Schlupfergebnisse bei Hühnern und Wassergeflügel. *Tierzucht* 14, 28-31, 1960.
- KALTOFEN, R. S., Over het keren der eieren tijdens het kunstmatig broeden (On turning the eggs during artificial incubation). Instituut voor Pluimveeteelt "Het Spelderholt", Beckbergen, Medeling No. 74, no date (1960).
- KODINECJ, G. A., Uljtrafioletova sprominjuvannja jačej v rizni stroki sezonu inkubacii (Ultraviolet radiation of eggs at different times of incubation). *Visn. sil'sjkospod. Nauk. ukr. Akad. sil'sjkospod. Nauk* 1958, No. 11, pp. 79-80, 1958. Quoted from *Animal Breeding Abstracts* 18, 457, 1960.
- KOSTIN, IG., (Results of the application of microdoses of gamma rays in the breeding of birds). *Biofizika* 5, 503-504, 1960.
- MCDONALD, M. W., Effect of temperature of storage and age of fowl eggs on hatchability and sex ratio, growth, and viability of the chickens. *Australian Journal of Agricultural Research* 11, 664-672, 1960.