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The Development of the Gonads in the Female and the Effects of Sinistral Ovariectomy and Bilateral Orchiectomy in the Japanese Quail (Coturnix coturnix japonica)

Jose Kannankeril
Loyola University Chicago

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THE DEVELOPMENT OF THE GONADS IN THE FEMALE AND THE
EFFECTS OF SINISTRAL OVARIECTOMY AND BILATERAL
ORCHIECTOMY IN THE JAPANESE QUAIL

(Coturnix coturnix japonica)

by

Jose Vacco Kannankeril

A Dissertation Submitted to the Faculty of the Graduate School
of Loyola University in Partial Fulfillment of
the Requirements for the Degree of
Doctor of Philosophy

June, 1964
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I. INTRODUCTION

Since the time of Goodale (1910), much work has been done on the effect of gonadectomy in birds. Because of the high degree of sexual dimorphism and easy availability, the domestic fowl has been used by the majority of investigators in this field. Domm (1924-) did the most extensive work on this problem and recorded in great detail the changes in primary, accessory and secondary sexual characters following ovariectomy and orchietomy in the brown Leghorn fowl. He observed that subsequent to sinistral ovariectomy (removal of left ovary), the right rudimentary gonad which is always present (Brode 1928) hypertrophies and depending on the nature of this gonad at the time of operation, it develops into either a testis, an ovotestis or an ovary. If ovariectomy is performed before the germ cells in the right gonad have disappeared, spermatogenesis may occur. The left oviduct generally remains in the juvenile condition until such time as the hypertrophied right gonad begins to secrete estrogen. Not infrequently, it becomes greatly distended with fluid, a condition spoken of as hydrosalpinx. The plumage becomes male in character and such individuals acquired a certain degree of masculine behavior as a consequence of the androgen secreted by the hypertrophied rudimentary right gonad. Subsequently, the plumage of most of these poulards, after a varying lapse of time, reverted
to the female or henny type. This reversion to the female type coincides with the production of estrogen by the hypertrophied right gonad. Following complete castration, regardless of age, the henny feathered poult again developed the male or capon type plumage. Implantation of ovaries or injection of estrogen into castrates brought about the development of the female plumage. These results show that the cocky feathering in the brown Leghorn fowl is the neutral type while the henny plumage is hormone controlled.

Similar experiments have been carried out in a few other species of birds but not always with similar results. Van Oordt and Junge (1933 a, b and 1936) found that in the ruff and in the black headed gull, the character of the plumage is controlled by the male sex hormone, while in the English sparrow (Keck 1934) no change in plumage occurs following either ovariectomy or orchietomy. Varying results are also reported in the case of pheasants and quails. Domm (1939), in preliminary experiments, found that in the common ring-neck pheasant and in the bobwhite quail ovariectomy resulted in the development of the cock plumage. In neither form was significant hypertrophy of the rudimentary right gonad observed. On the other hand, Witschi (1960), on the basis of limited observation and experiments, reported that in the Javanese fighting quail the control of sexual differences in plumage seems to be genetically determined.

These seemingly conflicting results in several species of
birds, and the fact that the above findings were based on limited experimental observations, led us to conduct an extensive investigation on the effects of gonadectomy in the Japanese quail (Coturnix coturnix japonica, Temminck and Schlegel).

Since we found no report on the embryology of the gonads in this species and since information on the extent of embryonic development and subsequent involution of the rudimentary right gonad is essential for a correct interpretation of the changes that might occur following sinistral ovariectomy, it was also decided to study the embryological development of the ovaries.

Hence, the purpose of the present investigation was twofold; 1) to follow the development of the ovaries with special reference to the fate of the rudimentary right gonad and 2) to study the effects of sinistral ovariectomy and bilateral orchietomy. It is considered that the present investigation will further our understanding on the development and physiology of the rudimentary right gonad and the factors controlling sex characters in birds.
II REVIEW OF LITERATURE

Development of the Ovaries

Little is known about the embryology of the Japanese Coturnix quail. Padgett and Ivey (1960) reported on the normal embryology but their study was limited to the pertinent changes in morphology from the first day of incubation to the day of hatching. A brief comparison of the day by day development with that of the chick and bob-white quail was also made. No mention was made of the development of the gonads or other visceral organs.

The embryology of the chick (Gallus domesticus) on the other hand is very well known. An elementary understanding of the embryology of birds was known to the ancient Egyptian, Indian, and Chinese people. The first fully preserved account, a detailed description of the chick embryo is credited to Aristotle (438 - 322 B.C.). In Book III, Chapter 2, and Book VI, Chapter 3 of his 'Historia animalium', Aristotle discusses the development of the chick, the formation of the egg from the 'septum transversum' and records other significant observations far in advance of his period. Although sporadic work has been done since then, it was during the Renaissance Period, that detailed accounts of the chick embryo appeared through the works of Fabricius (1621), Harvey (1651), and Malpighi (1672). A detailed account of these early works is, however, not necessary since very accurate and elaborate papers have been published in comparatively recent years.
Waldeyer's famous article, "Eierstock und Ei", which appeared in 1870, may be considered as the beginning of modern investigations relative to the sex glands of the fowl. In this paper the idea was advanced for the first time that the germ cells arise from the germinal epithelium a concept supported and refuted by subsequent workers.

Von Mihalkovics (1885) working on the embryology of the duck was the first investigator to observe the two proliferations which the germinal epithelium undergoes in the female. He designated the cells of the second proliferation as primordial eggs and the cells surrounding them as the follicular cells. Up to his time, the true sex cords were constantly confused with the rete cords both as to origin and function. He clearly pointed out that the rete cords arise from the wolffian tubules and the epithelium of Bowman's capsule.

Laulanie (1886) studied the chick embryo and concluded that the primordial sex gland was bi-sexual; that the germinal epithelium gave rise to the female component and that the male elements were present in the network of cords derived from the stroma in the middle of the gonad. According to him, the gonad was not indifferent but hermaphroditic. He believed that later in development one of the sexual elements degenerated and in consequence, the gland became male or female as the case might be. This idea now has only historical significance.

In 1887, Semon recorded his observations on the development
of the chick. He believed that the sex cords arose as outgrowths of the capsules of the Wolffian bodies. As Waldeyer (1870) did, he, too, saw two kinds of cells in the germinal epithelium, the columnar coelomic epithelial cells and the large clear primordial germ cells, the latter being derived from the former through successive changes. In embryos of about six days incubation, he saw sex cords grow out of the Malphgian body, reach the germinal epithelium and germ cells migrating into it. The germ cells later developed into sex cells and the small peritoneal-like cells gave rise to the supporting cells. Semon's paper is important in that he was the first to show a continuity in the chick between the primordial germ cells of the embryo and the male sex cells of the adult. This finding in the chick followed Nussbaum's (1880) observation of the same process in Rana and in Teleosts.

Prenant (1890) made a study on a complete series of chick embryos and observed the evolution of the gonad, particularly the histogenesis of the seminiferous tubule. An elongated ridge, covered with peritoneal epithelium, was noticed by him as early as three days of incubation on the medial surface of the Wolffian body, lateral to the root of the mesentry, which elevation he called the genital ridge. He believed that the germ cells could arise from the germinal epithelium and the stroma since he saw primordial germ cells in these two areas in 3½ day old embryos.

Soon after Semon, Hoffman (1892) came up with a magnificent work on his findings in about a dozen species of birds, mainly
taken from the group of Waders. His publication marks the beginning of an epoch in connection with research on sex cell formation for he found three species, Haemotopus ostralegus, Sterna paradisea and Gallinula chloropus, in which the germ cells did not originate from the modified germinal epithelium at least in part, if not completely. He argued that the germ cells which he called "ovules primitifs" have an extra gonadal origin for he saw these cells in the splanchnic plate of mesoderm in embryos as early as the twenty-three somite stage when the germinal epithelium was not yet formed. Although he failed to trace their ancestry, his work encouraged subsequent workers to trace the origin of germ cells and, as a consequence, led to a series of controversies between those who believed in the extra-gonadal and those who believed in the intra-gonadal origin of these germ cells.

Nussbaum (1901), Rubaschkin (1907), and Von Berenberg-Gossler (1912), were the pioneer workers who investigated the origin of the germ cells in the chick. They were able to find, in embryos of twenty-two to twenty-three somites, typical germ cells in the entoderm and splanchnic mesoderm lateral to the coelomic angle, some of which, in older embryos, had passed into the germinal epithelium.

d'Hollander (1904) studied oogenesis in the fowl and described in detail the changes, nuclear and otherwise, which the oogonia and oocytes undergo in the process of oogenesis. From the series of observations he made on embryos of ten days and
older, he concluded that the germinal epithelium gives rise to
epithelial buds, which grow down into the ovarian stroma. The
oögonia and primordial follicle cells arise from these germinative
epithelial buds, by a process of differentiation. He also
observed, that the period of multiplication of the oöcytes is
followed by a growth phase at about fourteen days of incubation
and that by the fourth day after hatching the oöcytes are en-
circled by the primary follicles. Careful observations were also
reported on the cytological changes that occur in the nucleus of
the oöcytes from the fourteenth day of incubation to the fourth
day after hatching.

One of the most complete and comprehensive studies on the
development of the gonad in the domestic fowl was made by Firket
(1914–1920). In his first publication which is Part I of this
series, he dealt with the formation of the genital ridge, the
development of the left ovary and discussed the origin of the sex
cells in the female. The development and subsequent cessation in
growth of the right gonad of the female, the organogenesis of the
testes and the condition of the genital organs of the adult are
described in Part II. From these studies, Firket concluded that
the rete testis arose from the mesenchyme between the germinal
epithelium and the mesonephric tissue and that their connection
to Bowman's capsule was secondary. He noticed the extra-gonadal
origin of the primordial germ cells but claimed that, in the
course of development, they degenerate and disappear. The
definitive oocytes of the adult, according to him, arise from the germinal epithelium. The germinal epithelium gives rise to two proliferations in the female - the primary and the secondary, the cells of the secondary later differentiate into the cortical portion of the ovary while in the male the cells resulting from the single proliferation give rise to the testis. He observed the retardation in growth of the right gonad in the female embryo but reported no evidence of its persistence in the adult.

Another important contribution to the development of the gonads in the domestic fowl was made by Swift (1914, 1915, and 1916). In these three papers, Swift discussed in detail not only the origin and development of the sex cords in both sexes, but also the origin and early history of the primordial germ cells and their role in the formation of the true sex cells. He was the first to show that the primordial germ cells in the fowl originate from the entoderm at the anterior and antero-lateral margins of the area pellucida of embryos beginning with the primitive streak stage to about the time of the three somite stage. These cells later migrated by way of the blood stream to the gonad where they developed into the true sex cells in both male and female. Like Firket, he, too, found an asymmetry in the distribution of the germ cells in the early gonads, which were about two to five times more numerous in the left gonad. The formation of medullary and cortical tissue from the germinal epithelium of the female and only medullary tissue in the male
were meticulously described.

The history of germ cells in the domestic fowl was also studied by Goldsmith (1928), who arrived at similar conclusions regarding the origin and migration of the primordial germ cells. This investigator maintained that there is no widespread degeneration of the primordial germ cells after their arrival in the gonad region, and that there is no transformation of somatic cells into definitive germ cells, an opinion contrary to that of Firket.

Essenberg and Garwacki (1938), working on the development of the chick in our own laboratory, emphatically deny the claim that the primordial germ cell gives rise to the definitive oocyte, and argue that the oocytes are derived entirely from the germinal epithelium.

Brode (1928) made a chronological study on the histological condition of the right and left ovary in embryos of the domestic fowl from nine days incubation to eighteen months post-hatch. This investigation established the fact that a rudiment of the right ovary is present throughout life in the brown Leghorn fowl. About 61% of the right rudimentary gonads in adults contained only medullary tissue while the remainder also revealed some cortical tissue. Normal primordial germ cells were found in the medullary tissue up to three weeks after hatching, following which they gradually disappeared or could no longer be recognized. The medullary cords persisted throughout the entire life cycle, either
as distended tubules or as isolated cords of modified epithelial cells.

Apart from the domestic fowl, embryological studies have been reported in few other birds. Blocker (1933) studied the embryology of Passer domesticus, where he traced the history of the germ cells, development of the indifferent gonad and sex differentiation. His work is important in that he brings out a conflicting opinion with respect to the origin of the medullary cords. He does not believe that the medullary cords are proliferated from the germinal epithelium and reports that,

"in Passer domesticus, no such formation of cords from the epithelium seems to take place. The epithelium of the early gonads as far as can be observed, remains of uniform thickness, consisting of two to three layers of flattened epithelial cells. The nuclei of the dense underlying mesenchyme tissue rearrange themselves in such a way as to give rise to indifferent gonad, the appearance of being made up of indistinct tubules or cords".

A similar view is held by Witschi (1935 a) from observations on the embryonic development of the chick, the English sparrow and the Red Wing Black bird. According to him, the indifferent gonads become organized during the fourth day. They consist of a cortex, derived from the strip of splanchnopleure above the coelomic angle and a medulla which arises from the blastema of the mesonephric cord. As to the asymmetry of the sex glands of birds, he argues that this is due to a primary, hereditarily fixed, deficiency of the right cortical inductor.

The embryonic history of the gonads of the white Pekin duck
is also known through the investigations of Burwell (1931) and Lewis (1946), (both names belong to the same person). She supports the extra gonadal origin of the germ cells and the epithelial origin of the medulla in the duck. In the latter work she studied the effects of several estrogens and an androgen on the development of the gonads and gonoducts. From her study on the effects of these hormones in the incubating egg, she concluded that cortical cords may form from the germinal epithelium of the left testis or from the primary testicular cords which have grown out and formed a layer on the surface of the gonad.

A comprehensive study of the literature regarding the occurrence of a right ovary and oviduct in birds was made by Chappellier (1913). He noted that the phenomenon is widespread, existing in birds of forty-four species belonging to twenty-nine different genera of ten orders. Fourteen cases were cited in which the right ovary was larger than the left ovary and two cases in which the left ovary was absent while the right was normal.

The condition of the urinogenital system in owls, at least in five different species examined, is quite similar to that found in the domestic fowl, in having an ovary and oviduct only on the left side (Domm - 1939). On the other hand, examination of seven species of hawks revealed bilateral development of ovaries in varying degrees. In Marsh hawks, *Circus hudsonius*, the right ovary is invariably present while several Red-tailed
hawks (Buteo l. lineatus) were encountered in which no right ovaries were found.

Stanley (1937), also presented evidence to show that certain species of the Falconiforms still retain the primitive type of bilateral ovaries which are of nearly equal size (Circus hudsonius, Accipiter cooperi). In other species of the same order, the right ovary is much reduced, retaining throughout life the appearance of a small rudimentary gland (Cathartes aura septentrionalis, Buteo p. platypterus). However, the majority of species are characterized by varying degrees of reduction of the right ovary forming a complete series from normal size to its virtual absence.

Working on germ cell migration in relation to asymmetry in the sex glands of hawks, Stanley and Witschi (1940), reported that as a rule the right ovary is largest in Accipitrinae and is progressively smaller in Falconinae, Buteoninae and Cathartidae. In the Strigidae, no right ovary was ever found. They also noticed a primary asymmetry in the distribution of the germ cells in the splanchnic plates prior to the formation of gonad primordia; the left side having a slightly higher number of germ cells. Further, in birds having a rudimentary right gonad, they found that the germ cells migrate from the right to the left side across the dorsal mesentery during differentiation of the gonad.

As for quail, so far as we know, no information is available as to the nature of the right rudimentary gonad.
Gonadectomy:

Since ancient times, people have been aware of the effects of castration in animals as well as in human beings. In the Orient and in early Greece the employment of Eunuchs - castrated human males - as Chamberlains of Royal courts has long been recorded. Similarly, castration of the bull for practical purposes was a common practice among cattle breeders all over the world. This was true with respect to the cock. For centuries castration of both sexes of fowl was practiced for commercial purposes and the more obvious consequences were described and pictured in the Historia animalium of 1555 by Conrad Gesner. However, scientific analysis of the effects of castration dates back only to the early part of the present century.

Ovariectomy:

Guthrie (1910) was probably the first to record the results of ovariectomy in post embryonic fowl. He was studying the survival of the engrafted ovary, when he noticed a case of degeneration of the graft in an ovariectomized bird and observed the following:

"The pullet rapidly acquired not only the outward anatomical features of the cock - the cock's comb, wattles, long hackle and tail feathers, rapidly developing spurs, carriage, etc. - but the behavior as well was that of a male; it exhibited a pugnacious attitude towards other cocks, was attracted by hens, and even went so far as to tread hens as a cock."
"removal of the ovaries from a young female is followed by a subnormal development of female characteristics including sterility. The general effect on development may be so strong that on reaching adult age, the unsexual animal may present qualities as strongly masculine as feminine."

It is surprising that he failed to notice the hypertrophied right gonad, for we now know that there must have been one, in his sex reversed fowl.

Leaving this chance observation of Guthrie, it was Goodale (1913, 1916), who first began a systematic study on the effects of ovarieotomy in domestic fowl. By carefully noting the changes in the plumage and other secondary sex characters, he concluded, apparently not aware of the results of Guthrie, that the female may assume male sexual characters following ovarieotomy. Goodale placed little significance on the hypertrophy of the rudimentary right gonad, for he found only nephrogenous tissue on histological examination of the right gonad.

Benoit was one of the early workers to repeat the work of Goodale on the fowl. Through a series of publications, (1923, 1924, 1926, 1932) he recorded extensive observations on the effects of ovarieotomy. Although, he reported on only two birds in his first attempt, (1923), he was fortunate in getting complete sex reversal in both cases. These two birds presumably developed all the external male characters, while internally on the right at the level of the adrenals in each was found a testis which,
on histological examination, showed spermatogenesis in some of their tubules.

As early as 1922, Zawadowsky had observed regeneration on the right side at the level of the adrenals in all of his ovariectomized birds, and correlated with this was a more or less complete assumption of male characters. In a later publication, (1926 a), on the effects of ovariectomy, he also reported spermatogenesis in the right hypertrophied gonad of one of his cases.

Pezard, (1922), states that he never observed regeneration on the right side in any of his hens. Later, however, Pezard et al, (1925), reported several cases in which the ovariectomized female, developed the plumage, head furnishings and spurs of the male, while internally on the left, in some, was found tissue which on histological examination revealed immature seminiferous tubules in the center and ovarian follicles at the periphery. No mention was made of the right gonad.

Finlay (1925) observed regeneration on the right in two ovariectomized birds. Greenwood (1925) studied these regenerated masses histologically and found that one was testicular in structure while the other was an ovotestis.

A more extensive and complete investigation on the problem of sex reversal in the domestic fowl was made by Domm. As early as 1924, a pioneer report on sex reversal following ovariectomy in the fowl appeared, which was followed (1927) by a 'report compendium' on new experiments in ovariectomy and the problem of
sex inversion in which he reported the results on one hundred and two cases. His experimental studies (1927) were divided into three sections: 1. the effects of complete removal of the left ovary, 2. the effects of incomplete ovariectomy, and 3. the effects of secondary operations; i.e., removal of regenerated and/or hypertrophied gonads. In all these cases, the effects on the hypertrophied gonad, if any, the accessory sex organs (oviducts and Wolffian ducts), secondary sexual characters such as head furnishings, plumage, spurs, size, behavior, etc., were meticulously observed and reported. The results may be summarized as follows: Removal of the left ovary always involved, sooner or later, development of a gonad on the right side (testis-like in all except two cases of ovary and one case of ovo-testis) which showed indications of secretion of male hormone and in most of the cases also female hormone at a later time. Growth of testis-like tissue was also found on the site of the removed left ovary, an observation not previously made. Ovariectomy tended to arrest the growth of the oviducts except when ovarian tissue was present or when the hypertrophied gonad began to secrete female hormone. In the presence of testis-like gonads, the Wolffian ducts responded by growth and often by coiling. Likewise, the head furnishings assumed the character and size of those of the normal male. The plumage changed to the neutral or capon type. Where the hypertrophied gonads also began to secrete female hormone, the plumage reverted to the female type, either completely and permanently or
only partially for varying periods. The latter may remain the intermediate stage indefinitely though many ultimately reverted to the neutral or male pattern. The molt of the poulards was frequently irregular and many of them did not pass through the regular molt of normal birds. The spurs developed in all ovariectionized females and in mature individuals they were usually as long as those of the cock, though their rate of growth varied somewhat. The behavior of poulards became strikingly masculine. Crowing, combativeness and courtship behavior were commonly observed and while treading attempts were frequent, copulation was only witnessed on a few occasions. Body size varied but, in general, it approximated that of the normal female being inferior to that of the cock or capon.

Incomplete ovariectomy resulted in a combination of male and female plumage, the greater the amount of ovarian tissue found at laparotomy or autopsy, the more pronounced were the female characters displayed.

The removal of all gonadal tissue resulted in poulards, similar to the capon in appearance and behavior.

Commenting on Domm's (1927) work, Lillie (1927) concludes that "the working hypothesis to which we are led by Domm's results is negatively, that there is no inversion of cells involved in the transformations that follow ovariectomy in the hen, or, positively, that the cells follow their embryonic determination throughout the entire series of transformation".
In none of Domm's (1927) poulards was spermatogenesis observed in the hypertrophied testis-like gonads. This was particularly baffling since Benoit (1923) and Zawadowsky (1926) had observed spermatogenesis in ovariectomized fowl, from a relatively insignificant number of experiments. There was, however, one reason for this difference in results. Domm had operated on older birds, mostly three to eight or nine months, while the above investigators had worked on younger birds. Brode (1928, vide supra) working in Domm's laboratory, found that the primordial germ cells disappear from the right rudimentary gonad of the fowl by approximately three weeks after hatching so that by the end of the first month they have disappeared or can no longer be recognized. Therefore, Domm (1929 b) made a systematic study on the effect of age at the time of operation on the occurrence of spermatogenesis in the poulard. In this series he observed spermatogenesis in 16 cases out of a total of 225 ovariectomized brown Leghorns. The majority of these had been ovariectomized prior to 30 days but several had been operated as late as 60 days of age. On the basis of this data, Domm (ibid) hypothesized that:

"primordial germ cells are necessary for gametogenesis and that when they become incorporated in the cords of the medulla, they produce spermatogenesis, and when in the cortical elements of the gonad they produce ovogenesis".

Padoa (1931) reported spermatogenesis in three of thirteen birds which had been ovariectomized at 75, 87 and 102 days of age, thus indicating that, if Domm's hypothesis is correct, germ cells
may occasionally occur in the right rudimentary gonad of the fowl beyond the age of 30 days.

Studying the materials from the experiments of Domm (1927), Gray (1930) traced the development of the testicular tubules in the hypertrophied gonads. He described four types of inter-tubular tissues: 1. fibrous connective tissue, 2. masses of lymphoid tissue, 3. various blood elements and 4. fat-laden cells. As for the source of the hormones secreted by these gonads, he argued that only to the medullary tissue can this function be logically attributed.

Once the basic effects of ovariectomy were understood, workers began to investigate the principles responsible for sex inversion in the fowl by other experimental approaches such as, implantation of gonads and hypophysis, introduction of hormones, etc. Domm (1928) tried transplanting rudimentary right gonads and hypertrophied right gonads into cocks and capons. Only a few of these transplants became successfully established and it was felt that the lack of genetic relationship between donor and host and the firm consistency of most of the engrafted gonads, which consequently did not lend themselves readily to vascularization, were factors responsible for the lack of success rather than an inadequate technique. On the other hand, in the three successful cases of transplantation of ovary into capons, it was found that contrary to some earlier observations of practically complete feminization, first the female and later the male characters
developed. This gave rise to the suspicion that the medullary as well as cortical elements had become activated in the growing graft. A similar attempt with normal testis grafted into bilaterally ovariectomized fowl (Domm 1929) showed that the host continued to retain its male characters, which observation led Domm to conclude that the normal testis and testis-like hypertrophied gonad behave differently in hormone production and its effects on plumage and thus confirmed his observations in the sinistrally ovariectomized poulard.

Domm (1931) implanted hypophysis into young female chicks, and found that the implants acted directly on the gonad tissues of the host producing a precocious endocrine, rather than gametogenetic function for he found no evidence of gametogenesis despite the fact that the sexual characters had been precociously developed. The right rudimentary gonads were not significantly affected by the implants. An effect similar to that of hypophyseal implantation was also reported by Domm and Van Dyke (1932) in young female chicks following daily injections of pituitary Hebin, an hypophyseal extract prepared from powdered sheep's pituitaries. On the other hand, injections of pituitary Hebin into capons (Domm 1933 b) did not affect either plumage or head furnishings. From this, the author concluded that the changes noticed in the former experiments were mediated through the gonads. Domm (1933a) injected pituitary Hebin in sinistrally ovariectomized fowl and found no effect on the rudimentary right gonad.
However, injections of this preparation in female embryos, forty-eight hours to nine days in age, brought about substantial development of the rudimentary gonad (Domm and Dennis 1937, Domm 1937). Thus it was found that the right gonad is responsive to Hel1in only in the early stages of development and non-responsive in later stages.

Injections of Pregnant Mare Serum (P.M.S.), Follicle-Stimulating Hormone (F.S.H.) and Luteinizing Hormone (L.H.) were shown by Taber (1948) to behave more or less the same as those of Hebin. Kornfeld (1953) and Kornfeld and Nalbandov (1954) studied endocrine influences on the development of the rudimentary gonad of the fowl. Exogenous estrogen and to a lesser extent androgen was observed to inhibit the growth of the rudimentary gonad of the ovariectomized fowl. Prolactin, similarly was observed to inhibit hypertrophy of the rudimentary right gonad in poulards and hypophysectomy significantly depressed the mean weight of this gonad. All attempts to accelerate growth of the right gonad in poulards, or to maintain it in ovariectomized hypophysectomized birds failed.

Taber et al (1958), working along similar lines, brought forth further evidence on the effect of estrogen and androgen on the rudimentary right gonad of ovariectomized poulards. In all these cases, inhibition was observed only in the medullary component of the right gonad while the cortical component, found in 20 to 30% of the cases (Kornfeld 1953, Taber et al 1958), was not
affected to any statistically significant degree. This fact led Gardner and Taber (1963) to conclude that inhibition of the right gonad (both medulla and cortex) by the left ovary, in normal birds must be affected not by the steroid-like estrogen or androgen produced by the left ovary, but by some other substance secreted by this gonad. The experimental evidence for this assumption was the fact that injections of extracts of acetone dried ovaries containing no detectable estrogen, according to them, brought about a statistically significant inhibition of the right rudimentary gonad. In the light of this evidence, it is significant to note that Kornfeld (1960) brought about, for the first time, an experimentally induced proliferation of the rudimentary right gonad in intact fowl by an anti-estrogenic agent, 17α - ethyl - 19 Nortestosterone (nilevar-Searle). These conflicting reports would seem to indicate that the mechanism by which the left ovary inhibits the right gonad is not yet completely understood.

Ovariectomy has also been performed on birds other than the domestic fowl but not always with similar results. The findings on ovariectomy and castration in some sexually dimorphic birds, including those which show seasonal variation in plumage, have been brilliantly reviewed by Domm (1939) and more recently by Witschi (1960).

In fancy breeds of chickens such as Sebright bantams, where the male and female are normally hen feathered, both sexes were observed to assume the cock plumage after castration (Morgan 1915-
1920, Eliot 1928). But as the right rudimentary gonad hypertrophied in the poulards, the plumage reverted to the henny type (Eliot 1928). Thus in this breed as in the brown Leghorn, the cocky plumage is the neutral form while the henny plumage of both male and female is the hormone controlled variant.

Athias (1928 a,b, and 1931) and Padoa (1931) performed ovariectomy experiments on the turkey hen and found that this operation did not change the plumage. However, Van Oordt (1933) and Scott and Payne (1934) performed similar experiments and found that such birds, after molting, assumed the neutral bronze plumage of the cock. Athias later admitted (see Van Oordt 1936) that his poulards assumed the neutral plumage at a later period. Neither Padoa (1931) nor Van Oordt (1933) observed any hypertrophy of the rudimentary right gonad.

Removal of the left ovary in the common pheasant (Phasianus colchicus) and also in hybrid females from a cross between the silver pheasant (Gennaeus nycthemerus) and the common pheasant was followed by the assumption of cocky plumage (Zawadowsky 1922, 1926b). Domm (1938, 1939) in a series of ovariectomies in the common ring-neck (Phasianus colchicus troquatus) found that the female assumed the cocky type of plumage but did not develop the brilliant red papillary skin found so conspicuously developed about the eyes of the male during the breeding season. Spurs did not develop either. No hypertrophy of the rudimentary right gonad was observed.
Similarly ovariectomy in Lobwhite quail (*Colinus virginianus*) has shown that the poulards develop the black and the white plumage markings characteristic of males. There was no hypertrophy of the rudimentary right gonad (Domm 1939).

Witschi (1960), based on limited observations and experiments, reported that in Javanese fighting quail (*Turnix pugnax*) the control of sexual differences in plumage is genetic.

Duerden (1919) recorded interesting observations on the ovariectomized ostrich in which the poulards developed the black plumes of the male. This author reported that since the latter are more valuable commercially, spaying of females is an enterprise practiced by some African farmers.

In birds showing seasonal sexual dimorphism, the results of ovariectomy are equally divergent. Ducks are a good example of birds showing seasonal sexual dimorphism. The female wears a henny-type plumage throughout the year but the drake displays two types of plumage. During the breeding season, he wears a plumage similar to that of the hen. After the post nuptial molt, a brilliant cock plumage appears, which is retained until the next breeding season. Removal of the ovary in the Rouen, Mallard or English Gray Call duck is followed by the assumption of the brilliant male plumage (Goodale 1910, 1913, 1916; Zawadowsky 1926b, Cavazza 1931, 1932). Witschi (1960) believes that a hypophyseal hormone, L.H., is responsible for cock feathering in the Mallard duck. In the normal breeding female, the steroid hormone produced
by the ovary checks the L.H. from manifesting its effect, but when the female hormone is lacking either due to the inactive state of the ovary or ovariectomy, the L.H. induces development of the cock plumage. Domm (1939) noted that the Rouen duck differs from the chicken in that the right gonad reveals hypertrophy only in exceptional cases.

In weaver finches (Euplectes species) the females constantly wear the typical henny plumage as in the Rouen duck. The male changes seasonally between a nuptial cock plumage and an eclipse hen plumage. Castration does not alter the cycle of plumage changes in the male. On the other hand, the same periodicity is established in ovariectomized female finches, (Witschi 1935 b, Levi 1936). Witschi (1960) interprets this result as in the duck, namely, that a hypophyseal hormone, probably L.H., is responsible for bringing forth the cock feathering and that in the normal female development of cock plumage is apparently prevented by the early release of ovarian estrogens. In the orange weaver (Pyromelana franciscana) the ovariectomized female does not molt preceding the breeding season, but when plucked the regenerating feathers are not of the henny type but of the male nuptial type. Plumage conditions in the red-billed weaver (Quelea quelea) were found to be identical with that of Pyromelana but its bill color was found to be controlled by the ovarian hormones.

An entirely different control mechanism is reported in the case of gulls and ruff. In the black headed gull (Larus
both male and female wear an eclipse and a nuptial plumage. Van Oordt and Junge (1933 a,b) found that castration arrests the development of nuptial plumage in the male which shows that this plumage is under the influence of androgens. No females were included in the experimental series but these investigators believe that ovariectomy would similarly prevent development of cock plumage in females. A similar phenomenon is reported in the ruff (Philomachus pugnax) by the above investigators (1936). Domm (1939) believes that in the above two groups of birds, the nuptial plumage that appears in the normal female is controlled by androgens elaborated by the medullary component of the ovary rather than by estrogen.

Keck (1934) found that the plumage of the English sparrow (Passer domesticus) is not modified by ovariectomy or the injection of sex hormones. The feather pattern in the sparrow therefore is apparently genetically determined.

Orchiectomy:

Although castration of the domestic cock has been a common practice for a long time, systematic studies of its effects on secondary sexual characters and behavior are not numerous. Sellhein (1898), Foges (1903), Pezard (1911, 1915), and Goodale (1913) stated that total castration does not alter the male type of plumage to any appreciable degree in the fowl. All agreed that the plumage of capons was more brilliant and abundant and some of the feathers longer than similar feathers in the normal male.
Goodale (1913, 1916) observed a disproportionate length in the primary coverts of capons when compared with those of the normal cock. Similar observations were reported by Domm (1939). Zawadowsky (1922) and Benoit (1929) actually recorded measurements on tail feathers of capons which showed a considerable increase in length over those of the male. These results indicate that the testis does exercise a certain degree of inhibition in the expression of male plumage. Castration experiments on turkeys by Athias (1928 a,b), Van Oordt (1931, 1933, 1936), Scott and Payne (1934), and Padoa (1931) on brown and silver pheasant by Pezard (1918), on common pheasants by Zawadowsky (1922) and Zawadowsky and Kritsch (1926) and on ring-neck pheasants (P. colchiiens troguatus) by Domm (1939) have all shown that in these birds, the male plumage is not altered by orchiectomy.

In sexually dimorphic birds with seasonal variation, castration experiments have shown divergent results. In the duck it has been found that orchiectomy prevents the male from assuming the henny plumage during the breeding season. These individuals retain the cocky plumage of the male (Goodale (1910, 1916), Zawadowsky (1922, 1929), Kuhn (1930), Caridroit and Regnier (1930) and Cavazza (1931, 1932)). Similarly, in the ruff and the gull, Von Oordt and Junge (1933 a,b, 1936) found that castration arrested the development of nuptial plumage. Thus we see that in these sexually dimorphic species, the male hormone is either directly or indirectly responsible for the assumption of the
breeding plumage in the males.

An entirely different mechanism of hormone control is seen in Finches. Witschi and his associates (1935 b, 1936) found that in the African weaver finch (Pyromelane franciscane) castration did not modify the rhythmical change of breeding and eclipse plumage in these birds. Similar results were obtained in the red-billed weaver (Quelea quelea) Witschi (1960) and in the English sparrow (Passer domesticus) Keck (1934). These results suggest a genetic rather than a hormonal control of plumage pattern.

There is general agreement among investigators that such characteristics as head furnishings, voice, courtship behavior and pugnacity are affected by castration. Domm (1927) observed that following bilateral orchietomy of the young adult, single comb, brown Leghorn fowl, the comb and wattles became pale and shrunken and decreased slowly in size. The spurs, on the other hand, showed a steady growth and the birds became neutral in behavior; they neither crowed, treded nor fought with other birds. Domm also observed that the accessory sexual organs of the male underwent regression following orchietomy. Similar observations were made in the turkey and some of the other birds mentioned earlier.

We are not aware of any similar reports on the effects of ovarietomy or orchietomy in the Japanese quail or other Coturnix species.

Adé Agostini (1936) by injecting follicular hormone (Serono's concentrated Oestrolase) at 500 t.u. per cc., into the male common
quail (Coturnix c. coturnix), observed that the dimorphic feathers of the female were controlled by this hormone. The spotted feathers on the lower neck and upper breast of the female developed in males as a result of the above injections while development of the black mento-gular band of the male was inhibited by the same hormone.

Nagra et al (1959) reported on the histogenesis and response to sex steroids of the cloacal glands in the Japanese quail (Coturnix c. japonica). In castrated males, these glands were reduced in size. The administration of male hormone (testosterone cyclopentyl propionate) in castrates caused hypertrophy of the cloacal glands and the musculature of the dorsal cloacal wall. These investigators made no mention of ovariectomy experiments on this bird.
The animal selected for the present investigation was the Japanese quail (*Coturnix coturnix japonica*, Temminck & Schlegel), one of the eight distinct races of the coturnix species recognized by Peters (1934). Its systematic position is shown below:

- **Order**: GALLIFORMES
- **Sub Order**: GALLI
- **Super Family**: PHASIANOIDEA
- **Family**: PHASIANIDAE
- **Sub Family**: PHASIANINAE
- **Genus**: Coturnix
- **Species**: coturnix
- **Race**: japonica

The Japanese quail was introduced into North America in substantial numbers a decade ago with the hope that it might become established as a game bird. Although they failed to survive when released in open country, they were found to be an ideal laboratory animal because they are hardy, relatively disease free, easily domesticated and very prolific. The incubation period is short (16 to 17 days), they mature rapidly and begin to lay eggs at around six weeks of age.

Most of our early stock of birds and eggs were obtained from
a reliable source*. Subsequent to this, we reared our own stock from birds hatched in our laboratory. Upon hatching, all chicks were placed in an electrically heated brooder and later removed to small rearing pens (13" x 13" x 8"), where they were kept in groups of from four to six birds. The chicks were fed a commercial game bird starter until three to four weeks of age and then growing mash until they began to lay after which they received laying mash and some chicken scratch consisting of cracked mixed grains.

The development of the gonad:

For the embryological studies on the gonad, fertile eggs were incubated at 100°F and the embryos sacrificed at one day intervals throughout the incubation period of 16 to 17 days. A number of specimens for each age group were examined grossly in order to form a quantitative estimate of the variability in normal development. The typical embryos of each group were then checked with the stages reported by Padgett and Ivey (1960). Post-hatch birds were sacrificed at one day intervals for the first ten days, then at two day intervals for the next ten and after this at five to ten day intervals up to maturity (45 to 60 days) and at random thereafter up to three and a half years.

The embryonic and post-embryonic specimens were examined under a dissecting microscope for gross features of the sex organs.

* Antelope Valley Game Farm, Lincoln, Nebraska. We also received a few birds from Dr. A. V. Nalbandov, Department of Animal Physiology, University of Illinois, Urbana, and Dr. R. K. Meyer, Department of Zoology, University of Wisconsin, Madison.
and after measurements of the primary and accessory sex organs were taken, the gonads were fixed for microscopic examination. The number of specimens observed macroscopically and microscopically are given in Tables I, II and III.

The selection of the fixing fluids and stains employed depended on the type of cells or tissues being looked for at the various stages of development. Although it was not the aim of the investigation to make a detailed cytological study of either the primordial germ cells or other cells in the developing gonad, an attempt was made at least with respect to the germ cells to differentiate them by histochemical methods. Chiquoine (1954) traced the germ cells in Mouse embryos by applying the Alkaline Phosphatase stain of Gomori (1946). A similar attempt was made by fixing early quail embryos in cold acetone and staining with Gomori's and Burstone's (1958) modification of alkaline phosphatase stain, but it met with only negative results. Meyer (1961), Domm and Clawson (1962) and Clawson and Domm (1963) demonstrated glycogen in the germ cells of early chick embryos by the periodic acid Schiff technic, after fixing the embryos in chilled Gendre fluid. The same method applied to quail embryos did not give satisfactory results. Hence, we employed the classical method of Swift (1914, 15, and 16) and other early workers, identifying the germ cells by their reported cytological characteristics. Bensley's (1911) acetic-osmic bichromate mixture was found to be a good fixative for embryos of early stages since it satisfactorily
preserved the cytoplasmic yolk inclusions in the primordial germ cells. Following Bensley's fixative, thin sections were stained in Bensley anilin-acid fuchsin—Wright's blood stain (Swift, 1915). Both early and later embryos as well as the gonads of post-hatch birds were fixed in Bouin's fluid and sections stained either in alum hematoxylin-eosin, iron hematoxylin-fast green or Mallory's triple (McFarlane, 1944).

Sections of embryos and gonads were made at 4 to 6μ thickness.

Measurements on gonads and accessory sex organs were made with a millimeter rule. Thickness of the tissues and diameter of cells was calculated from sections with the aid of an ocular micrometer.

Gonadectomy:

Forty-nine females were sinistrally ovariectomized at ages ranging from 2 days to 30 days post-hatch. Similarly, twenty males between 6 and 40 days of age were bilaterally orchietomized. Details of the ovariectomy experiments are given in Table IV.

The method of gonadectomy followed was essentially the one originated and used by Domm (1927). Birds were starved six to twelve hours prior to operation. Pentobarbital sodium (Nembutal), 0.3 to 0.35 mg/kilogram body-weight was administered intraperitoneally to produce general anesthesia. Birds were tied to an operating board lying on their right side and an opening was made into the body cavity between the last two ribs. The opening was retracted as far as possible without damaging the kidney and the
left ovary brought into full view by pushing aside the intestine with a wad of saline moistened cotton. The peritoneum covering the ovary was dissected away and all ovarian tissue removed as completely as possible by blunt dissection. Gelfoam pieces were used to keep the loss of blood to a minimum. Electrocauterization was used only occasionally where small remnants of ovary were found or suspected after the operation.

In the case of the male, the left testis was usually removed first and the right subsequently after the bird had fully recovered from the first operation. In a few cases, both testes were removed in a single operation through the left side. Special care was taken to make sure that no visible loose fragments of either ovary or testis were lost in the body cavity during the operation.

Records:

Primary and accessory sex organs: Poulards were sacrificed at intervals (see Table IV) and the condition of the hypertrophied gonad, if any, and oviducts and Wolffian ducts noted and their measurements taken. Then the sacrum with sex organs intact was preserved either in Formalin (10%) or in Alcohol (75%), the latter after fixation in Bouin's fluid. In the majority of cases, the hypertrophied gonads were sectioned at 4 to 6 μ and stained for histological study with either alum hematoxylin-eosin, iron hematoxylin-fast green or Mallory's triple (McFarlane 1944).

Capon were similarly sacrificed to check regeneration of
gonad tissue and the condition of Wolffian ducts. The sacrum and the skin with plumage intact were preserved in most of the cases.

**Plumage:** Weekly to monthly observations were made to determine what feather changes occurred as a result of gonadectomy. The examinations were concentrated on the sex dimorphic areas of the throat, lower neck and upper breast. Neck and breast feathers were plucked and preserved at intervals in selected cases to check the condition of the emerging feathers. When the birds were sacrificed, a record was made of the condition of the plumage. In some cases, the whole skin was kept with plumage intact and preserved with powdered alum or sodium fluoride, while in others only the head and a few feathers from each of the dimorphic area were kept and stored for further reference.

**Feather length and growth rate:** An attempt was made to determine whether there were any differences in growth rate or in length of identical feathers in the four experimental groups under consideration, namely: normal males and females, capons and poulards. The following feathers were selected for this purpose:

- 2nd and 3rd left primaries
- 2nd and 3rd left secondaries
- Left and right main tail feathers

The above feathers were plucked from a dozen fully grown birds for each of the four groups and the lengths measured with a millimeter scale. The newly emerging feathers were kept under observation and measured on 11th, 17th, 23rd and 35th day after plucking to
determine their growth rate.

cloacal gland: This structure was kept under observation to determine its degree of development in males, females, poulards and in capons. Subsequent to the sacrifice of poulards and capons, the cloacal glands from some of them were sectioned, histologically studied and compared with those of the normal male and female.

Body weight: Birds belonging to the four categories, namely: males, females, poulards and capons, but of the same age, were weighed at 2 to 4 day intervals prior to maturity and at weekly or monthly intervals thereafter to compare the growth rates of these birds.

Behavior: Efforts were made to observe possible changes in the behavior of poulards and capons. Individuals of a kind were kept in the same cage or they were placed together in various combinations with normal individuals to observe aggressive and treading behavior.
IV RESULTS

THE DEVELOPMENT OF THE OVARY:

A large number of embryonic and post-embryonic gonads were collected in order to make a careful study on the development of the ovary. The exact number of specimens examined both macroscopically and microscopically during the various stages of development is shown in Tables I, II and III.

The early history of the gonads: The formation of the gonads in birds may conveniently be considered as beginning with the arrival of the primordial germ cells in and underneath the peritoneal epithelium midway between the cranial aspect of the mesonephric ridge and the developing dorsal mesentery. This occurs in the Japanese quail at about 48 to 60 hours of incubation (fig. 3). The primordial germ cells found in the gonadal area at this time, apparently do not originate de novo since the same type of cell may be seen in other areas of the embryo (fig. 2), especially in the entoderm, the space between the entoderm and mesoderm, and in the dorsal mesentery, prior to their appearance in the gonadal area. It has been well established in the case of the chick (Swift 1914), that the primordial germ cells arise anterior and antero-lateral to the embryo in a specialized region of the germ wall entoderm just at the margin of the area pelucida, during the primitive streak stage and up to the formation of the third somite, and that they are found in the space between the entoderm and ectoderm.
Later, when the mesoderm arises, these cells, by ameboid movements, migrate into it and into the blood vessels being formed there. They are carried by the blood stream into the gonadal area as well as into other parts of the body (Swift 1914 and Firket 1914). It was not our intention to trace the origin and migration of the primordial germ cells in the quail, but we should call attention to the fact that our observations on the early stages of quail embryos, support the extra gonadal theory on the origin of these cells and their subsequent migration into the gonadal area as has been observed by others in embryos of the domestic fowl.

Characteristics of the primordial germ cells:

The primordial germ cells found in the early gonad and those observed in extra gonadal areas resemble each other in size, shape, and other characters. These cells are easily recognizable from the surrounding somatic cells by their immense size which is due to an increase in the volume of both nucleus and cytoplasm. They have an average diameter of 14 to 16 μ, which is retained throughout development although a slight decrease in size is noticeable in later stages but they never become so small as to be confused with somatic cells. As a rule, they are spherical in shape, although a number of them having oval outlines are usually seen in sections.

The large nucleus, which has a diameter of 7 to 10 micra, also reveals a spherical as well as an oval outline in sections and is usually eccentrically placed in the cytoplasm (fig. 2).
The nucleus is vesicular in appearance and much clearer than those of adjacent somatic cells. The nucleoli are distinct and clear and two of them are usually seen in each nucleus, often separated by a clear nucleoplasm. However, this is not a diagnostic character since neighboring somatic cells with a similar arrangement of the nucleoli are also found.

One of the most important diagnostic characteristics of the primordial germ cells of the early stages is the presence of numerous yolk granules in the cytoplasm. Embryos fixed in an osmic acetic-bichromate mixture, when stained with an Anilin acid Fuschin - Wright's blood stain combination, reveal these yolk globules as dark droplets in the cytoplasm of the germ cells (fig. 2). From the time the germ cells first appear, and during the period of their migration, they are loaded with spheres of yolk. As the embryo advances in age, the yolk material within these cells decreases in amount and by 5 to 6 days of incubation practically all the yolk granules have disappeared.

In embryos fixed in Bouin's fluid and stained with hematoxylin-eosin, the cytoplasm of the germ cells appears finely granulated and more vesicular than that of the neighboring somatic cells. In many germ cells, especially in those that were cut through the middle, the attraction sphere is visible as a condensation of cytoplasm, having a spherical to semicircular shape and resting usually on the nuclear membrane, on that side of the nucleus which is the farthest from the cell membrane. This
attraction sphere is not so prominent as to be considered an identifying character as was claimed by Swift (1914), in the case of chick embryo. Only by repeated and careful observation could the attraction sphere be observed in the germ cells of our quail embryos.

The only reliable way of identifying the primordial germ cells, as Goldsmith (1928) noted for the chick embryo, is by using a combination of all the characteristics listed above. By combining the large size, nuclear condition, presence of yolk material and the attraction sphere, can the cells under consideration be identified and clearly distinguished from the somatic cells.

Formation and differentiation of indifferent gonad:

As in other birds, the gonads of the quail develop on the medial surface of the mesonephros at the level below the mouth of the omphalomesenteric artery. At about 2 to 2½ days of incubation, when the germ cells begin to appear in the peritoneal lining of the gonadal area, thus converting it into the germinal epithelium, this epithelium is composed of one or two layers of cuboidal to columnar cells possessing oval or round dark-staining nuclei. Overlying the epithelium, a loosely arranged tissue of mesenchyme cells occupies the space between the germinal epithelium and the dorsal aorta (fig. 3). In 4 μ thick sections of the embryo, germ cells ranging in number from 2 to 3 are seen in the germinal epithelium and the overlying mesenchymal stroma. No difference, either in the thickness of the germinal epithelium or in the
number of germ cells, is evident between the left and right sides at this time (fig. 3).

By the third day of incubation, the first sign of a definite genital ridge appears in many embryos. These ridges can be faintly seen under a magnifying lens as elongated, narrow, whitish bodies on the medio-ventral side of the mesonephric ridge of either side. They are about 1.5 mm. in length and their anterior extremity begins some distance behind the cephalic extremities of the Wolffian bodies. By 3½ days of incubation, these ridges can be easily seen with the help of a hand lens.

On microscopic examination the genital ridges of 3 to 3½ day old embryos, especially in those of the latter, appear as rounded hillocks on the medial surface of the mesonephros separated from each other by the dorsal mesentery. Even at the first glance, it is usually noticed that the gonad is composed of three elements, the germinal epithelium, the stroma and the primordial germ cells. The germinal epithelium is 2 to 3 cells thick at its widest point, and is formed of columnar to cuboidal cells. The stroma overlying the germinal epithelium and occupying its concavity is made up of loose to densely packed mesenchyme cells resembling the general embryonic mesenchyme. The germ cells have increased in number (5 to 8 cells per section) and are located in the germinal epithelium as well as the stroma. The cytoplasmic yolk granules show up very well at this age.

An indication of bilateral asymmetry is noticed in certain of
the specimens examined, as concerns the number of germ cells as well as the thickness and size of the gonads; the left side being favored in each instance. In one of the sections of such an embryo there were 5 germ cells in the left and 2 in the right gonad. In some embryos, however, no such asymmetry was obvious at this time, the left and right gonads being more or less equal in size and in the number of germ cells.

By the fourth day the gonad has increased both in length and bulk and projects more into the coelom. It measures about 1.5 to 2 mm in length. The increase in bulk is due in part to the increased thickness of the germinal epithelium and also to an increase in the amount of underlying tissue. The germinal epithelium is 2 to 4 cells thick (fig. 4). In certain areas minute bud-like projections, from the epithelium into the overlying stroma, are apparent. This indicates the beginning of the primary proliferation of cords. By 4½ days this budding is clearly evident. The epithelial cells in the area of the bud are somewhat smaller than in the surrounding area, indicating that division of the cells has taken place. The mesenchyme forming the stroma of the gonad has become more compact.

In certain embryos an asymmetry in the thickness of the gonads was noticed while in others the left and right gonads were almost equal in size.

As regards the primordial germ cells, there has been practically no change in their size or appearance, except that the fat
globules are less numerous. The number of germ cells has, however, definitely increased from that observed in the younger stages. These are located in the germinal epithelium where they are more widely distributed. In embryos where the left gonad is larger than the right, the germ cells are also more numerous. In one of the heavily loaded sections of a 4 day embryo, the number of germ cells in the left gonad was 13 while there were only 6 in the right. Even in gonads of approximately equal size there was a slight predominence of germ cells in the left one.

By the fifth day of incubation the gonads are readily visible to the naked eye as short elongated ridges situated on the medio-ventral side of the mesonephros towards its cranial part. They measure about 1.8 to 2.0 mm in length, 0.3 mm in width and vary from 100 to 200 μ in thickness.

On microscopic examination one can easily see that active proliferation of the germinal epithelium has taken place (fig. 5). Some of the cords have already become detached from the epithelium in which case they lie encircled by the mesenchymal stroma. Each detached medullary cord contains a few germ cells distributed among the somatic cells derived from the germinal epithelium. The mesenchymal stroma at the hilus of the gonad remains as a compact mass but in other areas, it is scattered among the cords. In some of the gonads scattered capillaries filled with blood cells were seen in the stroma.

The primordial germ cells in general, retain their original
shape and size. A few of them, however, are somewhat smaller and this is apparently the result of mitotic division for germ cells in metaphase, though few in number, are noticed at this stage. One of the important factors concerning the germ cells at this stage, is that most of the inclusions of fat globules seen in the cytoplasm have almost completely disappeared. Hence, hereafter, the size of these cells will remain as the most significant identifying criterion.

Sex differentiation and development of the ovary up to the time of hatching:

By 5½ to 6 days of incubation formation of the cords of the first proliferation has ended and a definite determination of sex can be made. In addition to the left gonad in females being larger than the right, its germinal epithelium is also thicker (3-5 cells). In the right, at this time, it has diminished to little more than a single layer of cells (figs. 6 and 7). This thickening of the left germinal epithelium has occurred concurrently with proliferation of the primary cords. In the male, in both left and right testes, the epithelium at this time, has thinned out to a single layer as the first proliferation comes to an end.

Development of the ovary:

When the viscera are removed from the body cavities of female embryos of six days incubation, by which time sex differentiation has definitely taken place, the gonads are seen as conspicuous
white bodies lying on the ventro-medial surface of the pink mesonephroi. The disparity in size between the left and right ovaries, although it can be recognized, is not obvious to the naked eye. Both the left and the right gonad range from 1.4 mm to 2.0 mm in length and 0.3 to 0.6 mm in width. However, the disparity in size of the gonads, is distinctly evident when sections are examined under the microscope. The left gonad is thicker and this is due mainly to the extra thickness of its germinal epithelium (fig. 6).

The germinal epithelium of the left ovary is 3 to 5 cells thick at this stage and measures about 25 to 30 μ. The epithelial cells are columnar where the epithelium is thickest while in the thinner areas they tend to be cuboidal in shape. Among the epithelial cells numerous primordial germ cells are found whose number may vary from 8 to 12 in a single section. In two specimens of six days incubation, the germinal epithelium at the medio-ventral angle of the left gonad, was not only noticeably increased in thickness, but it also showed lobulations into the medulla from its inferior surface. The number of germ cells in this area also shows a considerable increase due to mitotic activity. This is the beginning of the second proliferation or formation of the cortical cords (fig. 7).

The region of the gonad under the germinal epithelium, which is called the medulla, is composed in greater part of medullary cords derived from the first proliferation. In a cross section, the medullary cords show up in different shapes and sizes. Some
are circular in outline, apparently representing cross sections, while others are elongated oval shaped and appear to be cut obliquely or longitudinally. Most of the cords seem to converge towards the hilar area of the gonad. As in the previous stage, the cords are formed of epithelial cells and some germ cells. The mesenchyme cells now fill the intercordal spaces.

The cortex and medulla are clearly separated by a connective tissue stroma derived from the mesenchyme cells of the ovary. Thus the primary tunica albuginea is visible as early as 6 days of incubation in the case of quail embryos (fig. 7).

In none of the six embryos examined at this stage was a definite cortex observed in the right gonad. Instead, its surface was covered by a cuboidal epithelium which in places was two layers thick (figs. 6 and 7). Few germ cells were seen in this layer and occasionally two or three were seen together.

The medulla of the right ovary resembles that of the left in structural detail except that in the right, the tissue is less compact. Germ cells are present in the cords as well as in the stroma of the right gonad, but they are definitely fewer in number than in the left. As in the left gonad, a primary tunica albuginea is visible under the germinal epithelium.

There is no significant change in the ovary of embryos of 7 days from that observed on the previous day, except that the cortex of the left ovary has increased in thickness and proliferation of the cortical cords has become more active. Mitotic divisions
have increased the number of germ cells in the cortical area. The medulla of the left ovary has also increased slightly in thickness due to mitotic activity of the cells, as well as by an enlargement of some of the cortical cords, especially towards the hilar area, as a result of the acquisition of a lumen. Mitotic division of some of the germ cells located in the medulla was also noted. The thickness of the medulla varied from 170 to 190 μ and the cortex from 15 to 25 μ.

The germinal epithelium of the right gonad is now composed of only a single layer of cuboidal to squamous cells. Sporadically scattered germ cells are still seen in the epithelium. The medulla of the right gonad, at least in some of the specimens, has increased in volume and measured approximately 130 μ in thickness which is about 10 to 15 μ thicker than on the previous day. As in the left ovary, lumina have now appeared in some of the medullary cords.

By 8 days of incubation, a sharp difference in size between the two gonads is visible. Although the length of the left gonad has remained more or less the same (2 to 2.1 mm), its width has increased up to 1 mm while the right gonad has not shown an increase over that of the previous day.

The cortex of the left gonad has thickened and is actively proliferating cortical cords. The maximum activity of cord formation is noticed at the medio-ventral side of the ovary. One of the most obvious features of this stage is the active division of
the primordial germ cells which show large numbers of mitotic figures. The resulting daughter cells are smaller than the original and show no cytoplasmic fat deposits. It is difficult to see the cytoplasmic outlines of these cells. They often appear to lie in a syncytium. The best way to identify them is by the characteristics of their nuclei. These are spherical in shape and in stained sections appear highly vesicular with a clear nucleoplasm except for a few aggregations of chromatin granules. The size of the nuclei varies from 4.5 to 5.5 μ (fig. 8).

There has also been a considerable increase in the size of the medulla of the left ovary and the fact that it continues to increase in size is obvious from the presence of dividing cells both in the medullary cords as well as in the inter-cordal mesenchyme. Distension of the medullary cords due to lumenization, as well as the loose arrangement of the mesenchymal cells, also contributes to the enlargement of the medulla (fig. 8). Most of the medullary cords are compact and their outline is readily distinguishable. Some of the cords, however, have a loose appearance and often fail to show a sharp boundary in cross section. In fact, some of them appear to be disintegrating. At the same time the individual cells of some of these cords have undergone certain changes in their cytoplasm which has become vesicular and vacuolated and thus they resemble the 'fat laden' cells described in chick embryos by Brode (1928) and others. The tunica albuginea that separates the cortex from the medullary tissue is clearly
visible in most of the specimens examined.

As for the right gonad, the most noticeable feature is that it has ceased to grow and actually shows indications of involution. The germinal epithelium has thinned out into a single layer of flattened cells whose nuclei project onto the surface. Primordial germ cells are very seldom seen in this epithelium.

The medullary tissue of the right gonad is less dense and more vacuolated than that of the left (fig. 9). The medullary cords have undergone the same modifications and changes that were noticed in the left ovary. Germ cells are seen in the cords as well as in the mesenchyme and few of them show mitotic divisions. The number of these cells seen in sections of the right gonad varies from 2 to 10. Between the medulla and the germinal epithelium a thin layer of connective tissue, the primary tunica albuginea, is visible.

The left ovary shows a further increase in both length and breadth on the ninth day. It averages from 2.8 to 3.0 mm in length and about 1.0 mm in breadth. Most of this increase is due to additional proliferation of the cortical cords. The cortex itself now has a thickness of 100 to 110 μ. The germ cells located in the cords multiply rapidly giving rise to daughter cells which, when ceasing to divide mitotically, give rise to oögonia. As a result of this proliferation, the germinal epithelium has thinned out in certain areas where a connective tissue stroma intervenes between the epithelium and the detached cords. This is the pre-
cursor of the secondary or true albuginea of the ovary.

The medulla of the left ovary by the ninth day has undergone certain structural changes. As was seen in the previous stage some of the medullary cords have acquired a lumen. Constituent cells of these cords have become cuboidal in shape and line the lumen. Another group of medullary cords has disintegrated into isolated as well as small groups of cells lined by a basement membrane. The rest of the medullary cords for the time being remain as compact units. The cells in most of these cords become vesicular and resemble the so-called 'fat laden' cells. A similar modification was also noticed in the cells derived from the disintegrated cords.

The right gonad has definitely begun to involute by nine days of incubation. It is smaller than in the previous stage in both width as well as in thickness. The germinal epithelium is made up of a single layer of cuboidal to squamous cells. Germ cells are no longer observed in the epithelium. The medullary tissue reveals the same modifications as seen in that of the left ovary, except that here it is more vacuolated and more loosely arranged. Many of the epithelial cells in the medulla show small and shrunken nuclei obviously suggesting atrophy of these cells. Germ cells, although few in number, are still seen.

Not much change over the previous day is seen in the left ovary of ten days except that it has increased in size. Additional proliferation of cortical cords is evident. The secondary tunica
albuginea is better developed and in places separates the germinal epithelium from the cortical cords. The texture and composition of the left medulla is practically the same as that of the previous day. The cells lining the distended cortical cords have become more flattened due to an increase in the size of the lumen.

The right gonad has decreased still further in size especially in thickness. The germinal epithelium was single layered in all four specimens examined at this stage. The medullary tissue has become more and more porous and more disintegration of medullary cords was noticed. From 5 to 10 germ cells are still seen in certain sections.

The average size of the left ovary at eleven days is about 3.0 mm in length and 1.5 mm in width. The right gonad, although it may extend up to 3.0 mm in length, is narrow and ranges from a width of 0.2 to 0.6 mm. It is firmly attached to the median ventral, surface of the mesonephros.

The most outstanding feature at this stage of development of the left ovary is the fact that the oögonia have entered into the first phase of meiotic division thus converting them into oöcytes. Those that lie at the inner aspect of the cortex have undergone a considerable change in their nuclei. The nucleus has enlarged somewhat in size and shows definite, deeply stained, chromosomes similar to those seen in leptotene stage of meiosis. In most of the cases the chromosomes are polarized, that is to say they are not distributed randomly but lie clumped to one side with a clear
space at the opposite pole of the nucleus (fig. 10). This arrangement is known as synizesis. Meanwhile, the germ cells on the outer border of the cortex are still undergoing mitotic division and thus new cortical cords are still being produced. The germinal epithelium in certain places has now become thin and is composed of three to four layers of prismatic to columnar epithelial cells.

The medulla of the left ovary has become more and more spongy due to the irregular arrangement of the lumina of the medullary cords and other vacuolar spaces that appear in the stroma. More and more degeneration of the medullary cords with a consequent increase in the 'fat laden' cells is observed (fig. 10). A few of the germ cells located in the medulla are also seen to be undergoing the early meiotic changes similar to those observed in the cortex.

The right gonad has undergone a further reduction in thickness (fig. 11). The germinal epithelium has flattened and is composed of a single layer of squamous cells. The medulla, as in the left gonad, consists of luminated cords, scattered groups and isolated epithelial and 'fat laden' cells, and mesenchymal stroma cells. Sometimes 3 to 4 germ cells are seen in a single section but none of them show any signs of meiotic division.

Not much change from the previous day is noticed in the left ovary on the twelfth day except that more and more oogonia, starting from the inner border to the periphery of the cortex, are
transforming into oocytes. Mitotic divisions of the germ cells were observed in the outermost area of the cortex especially near the borders.

The medulla of the left ovary, in most of the cases examined at this age, is almost encased due to the overlapping growth of the cortex on all sides except where it is attached to the mesonephros. The porous nature of the medulla has increased and the lumen of the cords in many cases reaches all the way to the area of the primary tunica albuginea. Isolated and groups of 'fat laden' cells are prominent. Capillaries with blood islets are also seen in the medulla. A few of the germ cells located in this area are also undergoing the changes of early meiosis.

The right gonad at this age is further reduced in size. The thickness of one of the specimens of medium size was only 85 μ. The germinal epithelium is single layered and continuous. 'Fat laden' cells and a few germ cells are seen in the atrophying medulla.

The continued transformation of more and more oogonia into oocytes is the principal change noticed in the left ovary of embryos of thirteen days. As the new cells from the peripheral area enter into the leptotene stage and reveal the synizesis arrangement of the chromosomes, those in the inner aspects of the cortex undergo the further stages of the early meiotic prophase. In some of these the chromosomes have loosened themselves and lie scattered in a network, filling the whole area of the nucleus. This
is the stage at which the oöcyte begins to grow. Meanwhile, the germinal epithelium has thinned out still further. A secondary tunica albuginea of connective tissue separates the cortical cords from the epithelium in most of these areas. At the lateral and medial border, as well as at the caudal and cranial ends of the ovary, proliferation of cortical cords continues due to the mitotic activity of the germ cells.

The medulla greatly resembles that of the previous stage. Two to three germ cells, some of which are in the leptotene stage, may be found in each section of the left ovary.

The thickness of the right gonad in some cases has been reduced to 50 μ. The germinal epithelium is flat and resembles the peritoneal lining of any other area of the body. The medullary tissue is very porous due to the irregular arrangement of the lumina and vacuoles. Isolated cells with small and shrunken nuclei are seen throughout the medulla. Occasionally, such cells are found in the lumen of the cord. Apart from these degenerating medullary cord cells, a few germ cells and clumps of 'fat laden' cells are scattered throughout the mesenchymal stroma.

The left ovary on the fourteenth day is very similar to that of the previous day. Most of the oögonia have now transformed into the oöcytes, except those at the edges of the ovary where mitosis of the germ cells is still taking place. The older oöcytes situated in the interior of the cortex are showing a certain degree of enlargement and thus beginning the growth phase. The secondary
tunica albuginea is clearly visible and separates the germinal epithelium from the underlying cortex. Two to three germ cells may still be seen in the medulla of most of the ovaries examined.

The rudimentary right gonad shows further reduction (fig. 12). Its size varies considerably in different specimens. The covering germinal epithelium is thin. Germ cells are absent in some of the sections while one or two may be seen in others.

The fifteenth day reveals no substantial change in the texture or composition of either the left ovary or the right gonad. In the left ovary more of the remaining oögonia have developed into oöcytes. Mitotic divisions of germ cells occur at the edges of the ovary and scattered germ cells may still be seen in the medulla.

The germinal epithelium of the right gonad is thin. Germ cells are still present although fewer in number than in the previous stage.

In the sixteen day embryo, the day on which they begin to hatch, the left ovary is seen as a whitish auricular shaped structure, about 4.0 mm in length and 1.5 mm in width, lying on the ventro-medial surface of the left mesonephric rudiment. Its cranial end partially conceals the left adrenal gland. The medial side of the ovary overlies a portion of the dorsal aorta, the basal portion of the postcaval vein (inferior vena cava) and the terminal part of the left iliac vein.

The right gonad, in contrast to the left, is much smaller,
1.5 to 2.0 mm in length and about 0.5 mm in width, and is attached to the medial side of the right mesonephros, generally gaining attachment to a portion of the postcaval vein and a part of the right iliac vein.

When microscopically examined, it is seen that the major portion of the left ovary is composed of the cortex which encases the medulla with its marginal folds except at the hilus where the medulla is attached to the mesonephros. The cortex now may show a thickness of 120 to 180 μ while that of the medulla ranges from 100 to 120 μ.

The germinal epithelium is thin and composed of 1 to 3 layers of cells which exhibit different shapes ranging from squamous to cuboidal, prismatic, and columnar. It occasionally is thicker between the cortical cords where the epithelial cells sometimes protrude deep into the intercordal area. A thin connective tissue layer, the true ovarian tunica albuginea, separates the epithelium from the underlying cortical cords. In the cortical cords, all of the oögonia have by now developed into oöcytes, except at the edges of the dorsal folds of the cortex, where conversion of the oögonia into oöcytes is still taking place. The older oöcytes in the deeper part of the cortex have grown in size and some of them are surrounded by epithelial cells derived from the germinal epithelium (fig. 13). This is the beginning of follicle formation. The nuclei in some of these oöcytes have grown to a size of about 7.5 to 10 μ in diameter.
The medulla as a whole looks very spongy, especially towards the hilus, due to an irregular arrangement of the lacunae and vacuoles. It is composed of four types of cells. The most prominent are the ones derived from the medullary cords which have not undergone any drastic modification. These line the lumen of the distended cords and are also found in loose aggregations, especially toward the outer portion of the medulla. The cells lining the lacunae, have smaller and somewhat shrunken nuclei as compared with the healthy looking nuclei of other cells. The 'fat laden' cells constitute the second type. They are seen, as in earlier stages, either as aggregated groups of both small and large size or as isolated cells. The cytoplasm of these cells in hematoxylin-eosin preparations, is clear and highly vacuolated with their small nuclei eccentrically situated. The third type of cells are the connective tissue cells derived from the mesenchyme of the early gonad. These cells assume various shapes; some are elongated and spindle shaped while others are oval in outline. The shape of the nuclei also varies from elongated oval to spherical. These cells are seen throughout the medulla between the medullary cells, islets of 'fat laden' cells, and the medullary cords when present. The islets of blood cells form the fourth type of cell found in the medulla. The blood supply of the ovary varies from individual to individual some having a seemingly greater supply than others. The capillaries of the medulla penetrate the cortex and may be seen between the cortical cords.
Germ cells were not observed in the medulla of the left ovary in any of the four cases examined histologically. The primary tunica albuginea was less well defined than in the previous stage. The right gonad at this stage is a rudimentary structure. The germinal epithelium that envelopes the gonad is thin, single layered, and composed of squamous cells. No cortex was observed in any of the four specimens examined. The medulla was composed of the same type of cells as was the medulla of the left ovary, namely, medullary cells, 'fat laden' cells, mesenchyme connective tissue and very few, if any, blood cells. The medullary cells were haphazardly scattered, and many of them showed a degenerative tendency with small and shrunken nuclei. The 'fat laden' cells occur in smaller groups than in the left medulla (fig. 14). About 15 to 20 such groups may be found in a cross section of the gonad.

Germ cells, although few in number, were still present in the right gonad. In one instance of ten consecutive sections of 4 μ, two sections showed two each; four, one each; and the remaining four sections, no germ cells at all. The nuclei of the germ cells are still much larger than those of the surrounding cells, however, they are smaller than the nuclei of the germ cells found in earlier stages. The cytoplasm of these cells is less well defined.

Post-Hatch Stages

From 1 to 10 days of post-hatch:
A detailed investigation on the growth and development of the left ovary, during the post-hatch period, was not intended hence
only certain pertinent changes will be noted throughout this period.

Although the left ovary does increase in volume with each passing day, this is not readily evident from examinations of its length or breadth in the early days. This is due to the folds that may appear on the surface of the ovary even as early as the time of hatching. The ovary has a pitted appearance by 8 to 10 days, due to the emergence of the developing follicles on its surface. Some of the large follicles at this period may measure up to 200 to 240 μ in diameter.

The germinal epithelium of the ovary remains single layered and composed of cuboidal cells. The conversion of the oogonia into oocytes appears to be complete in all areas of the cortex by the day after hatching. Even as early as the day of hatching, the growing oocyte may be surrounded by a follicular covering. Many of the oocytes die and disappear. Their disappearance is evident in the left ovary on the day of hatching for a decrease in number is noticed at this stage. It is apparent that the oocyte has undergone a slight increase in size before it disappears. The formation of the ovarian follicle as well as degeneration of oocytes first begins along the median ventral line of the ovary and then spreads to other areas. Follicles may be seen all over the ovary by the eighth day after hatching.

Apart from those that encircle the ovum and form the follicle cells, or the future granulosa cells, there are large
numbers of epithelial cells which begin to appear in the stroma of the ovary immediately after hatching. Some of these cells begin to enlarge in size. Their cytoplasm becomes vesicular and vacuolated resembling the 'fat laden' cells of the medullary area. These are designated as the "interstitial cells" of the ovary. Such modified cells may remain isolated or form clusters of different shapes and sizes. In the 8 to 10 day old ovary, these cells are particularly noticeable in the thecal layer of the growing follicle. The remaining unmodified epithelial cells fill the stroma and show a tendency of becoming elongated and fibrous in nature in older ones. As the folds appear in the ovarian cortex, the medulla is pulled and stretched to extend into the curves and loops of the cortex. As a rule, germ cells are not seen in the medulla after hatching. However, in one specimen of four days, a few germ cells were observed in some of the sections. The number of 'fat laden' cells in the medulla decreases with advancing age so that in 10 day old ovaries these cells are seldom seen.

The right rudimentary gonad: In the period up to 5 to 6 days after hatching, the right rudimentary gonad was visible to the naked eye in most of the specimens examined. It lies on the ventral face of the postcaval vein and/or the medial surface of the mesonephros, extending to a variable length of 1.0 to 2.0 mm and a width of 0.2 to 0.6 mm. After 6 days it is usually so small, in most cases, that it can only be detected by very careful examination.
A thin germinal epithelium which is occasionally discontinuous envelopes the right gonad. In none of the twenty-five gonads histologically examined during this age range was a cortex seen. The medulla consists of fewer and fewer numbers of cells (fig. 15). The amount of tissue left in the gonad varies considerably especially in the older ones. The epithelial cells derived from the medullary cords undergo further regression and atrophy. By the tenth day, these cells have the appearance of loose connective tissue or mesenchyme like cells. The connective tissue cells derived from the mesenchyme stroma of the medulla are indistinguishable from the epithelial cells. Some of these tend to become fibrous in nature. The 'fat laden' cells also decrease in number as the individual gets older. They were completely absent in two cases 9 and 10 days of age, while two other cases of the same age showed groups of such cells. Germ cells were still seen in the right gonad 3 to 4 days after hatching. However, after 4 days they were no longer found except possibly for an occasional shrunken nucleus whose identification was doubtful.

From 11 days to sexual maturity i.e., 45 to 75 days:

Left ovary: The structure of the left ovary remains basically the same as that of the ovary already described for 10 days. The most significant change noticeable in the growing ovary is naturally the continuous enlargement of some of its follicles of which the primary ones attain full grown size and rupture between 45 to 75 days. Not all follicles that begin to grow attain full size. Some
of them become quiescent after a slight growth while others undergo atretic changes and disappear. The space between follicles is filled with stromal tissue which consists of an abundance of fibrous connective tissue, especially in the older ones, and the "interstitial cells" found in aggregated groups as well as individual cells. The theca interna of the follicles is loaded with these "interstitial cells". However, they are missing from the theca interna of atretic follicles, where the theca is wholly composed of fibrous connective tissue cells. Whether the "interstitial cells" actually disappear or transform into the connective tissue cells could not be determined from this study.

The medulla of the left ovary becomes more and more fibrous and spongy as the ovary reaches maturity. The epithelial cells derived from the medullary cords, as well as the 'fat laden' cells, may be seen in the strands of the medulla up to 30 or 40 days of age, but as the ovary gets older, these cells are hardly noticeable among the heavily fibrotic strands of the medulla. Scattered nuclei of fairly large size may also be seen in the medulla, but their identity as germ cells is questionable.

**Rudimentary right gonad:** The rudimentary right gonad is no longer visible as a distinct delimited body. It may, however, be seen under low magnification as a narrow, elongated strand of tissue lying on the ventral surface of the postcaval vein medial to the right mesonephros. The size as well as the composition of this organ varies with individuals. It may be composed of a loose mass
of epithelial cells derived from the original medullary cords, connective tissue fibres, a few 'fat laden' cells, and the infiltrated blood cells (figs. 16, 17 and 18). In two cases of 50 and 75 days, lymphocytes were also noticed in the stroma. Fibrous connective tissue cells are more prevalent in the older stages. In some, the bulk of the gonad was found to be formed of cells of a fibrous nature with very few epithelial cells. In such cases, it would seem likely that either the epithelial cells have disappeared or that they became transformed into fibrous connective tissue-like cells. The number of 'fat laden' cells also shows considerable individual variation and in some cases one has difficulty in finding any. In none of the twenty-eight gonads studied in this age group, were germ cells observed although some large nuclei of questionable identity were seen. A thin peritoneal-like epithelium, which is discontinuous in some areas, envelopes the gonad. There was no indication of either a cortex or a proliferating epithelium in any of the gonads.

The rudimentary right gonads in older birds:

The right gonads of six older females (230 days to 3½ years) were studied histologically. A rudimentary gonad was present in all of these. Epithelial cells were fewer in number when compared with younger stages, but more fibrous connective tissue was present. The 'fat laden' cells found in the gonads of younger birds were rarely seen in any of these. In two of the six cases masses of lymphocytes were also seen.
HISTORY OF THE MULLERIAN AND WOLFFIAN DUCTS

Mullerian ducts: The tubal ridge that later contributes to the formation of the Mullerian ducts is visible at about 3 days incubation as a thickened area of peritoneum all along the dorso-lateral side of the mesonephros lying immediately lateral to the mesonephric duct. By 3½ days the cranial part of the ridge begins to invaginate to form a groove which soon transforms into a tube, the Mullerian duct. The tube is open at the cranial end but closed caudally. The part thus formed is relatively short. The major portion of the duct is formed by a posterior elongation and it reaches the cloaca at about 6 to 6½ days incubation.

In the female embryo development of the oviducts is uniform on either side up to 8 days at which time both ducts show a length of 6.0 to 6.5 mm. At this time the right Mullerian duct ceases to grow and begins to atrophy. The cessation in growth commences at the cranial end and by the fourteenth day it has disappeared except for a short cloacal stump of about 2.5 to 3.0 mm in length. In adult females this rudimentary cloacal oviduct may be found attached to the right side of the cloaca. It is responsive to female hormones so it may be somewhat larger in adults.

The left oviduct on the other hand continues to grow in the remaining embryonic as well as the early post-hatch period (Table 3). Between 35 to 45 days a tremendous increase in size and coiling takes place in preparation for ovulation. An increase in its vascularization is also noticed at this period. At the
time of ovulation the oviduct is large, vascular and convoluted and takes up most of the space on the right side of the body cavity between the ovary and the cloaca.

It is of interest to note in this connection that in the male retrogression occurs simultaneously in both the left and right Mullerian ducts and that it begins rather suddenly at 7½ days of incubation. Unlike the female, atrophy of these ducts begins at the caudal end and progresses cranialwards. This takes place rather rapidly, for by the eleventh day they have practically disappeared by the thirteenth day.

Wolffian ducts: The pronephric duct which later becomes the mesonephric duct, persists in the adult female as a straight thread-like structure lying in close association and parallel to the ureter on the ventral surface of the metanephric kidney (fig. 19). Anteriorly it is connected to the mesonephric remnant, consisting of a few convoluted tubules, the epoophoron, and posteriorly to the cloaca.
The effects of sinistral ovarioectomy:

Introduction: Forty-nine young quail were sinistrally ovarioctomized in order to study the effects on the rudimentary right gonad and the accessory and secondary sex characters (Table IV). All our operations were complete in that no regeneration of ovarian tissue occurred on the left side, as determined by examination at autopsy. In a few cases there was regeneration on the site of the removed left ovary, however, this was found to be testis-like rather than ovarian in character, the histological findings on which will be discussed elsewhere.

Removal of the left ovary resulted in some hypertrophy of the rudiment on the right side at least in the majority of the cases. This hypertrophy was, however, in no way comparable in magnitude to that observed in the domestic fowl under similar circumstances (Domn, 1927). In 10 cases the compensatory growth on the right side if any, was insignificant for only microscopic strands or patches of gonad tissue were seen (vide infra).

Macroscopic observation of right gonad: The hypertrophied right gonad in all cases occurred on the site of the normal right gonad which was described in the section on the development of the gonad. The size and shape of these gonads varied considerably. Some of the better developed ones have the general appearance of an embryonic testis, being elongated and rod-shaped (fig. 20). The contour of the free surface of such gonads was generally smooth and
the maximum size attained was 8.0 mm in length, 1.5 mm in breadth and about 300 μ in thickness.

The majority of the compensatory gonads, however, had the shape of an elongated disc. The peritoneal surface was smooth although a few of them had a wavy to pitted appearance. A few of them had the shape of an inverted L, with their long axis parallel to the mesonephros and the short arm lying horizontally across the cranial border of the mesonephros. In a few cases, the gonad was composed of two separate masses arranged in tandem fashion (fig. 21). In the cases of doubtful hypertrophy, the gonads, under magnification, were seen to be thin narrow sheets of tissue stretching from the medial surface of the mesonephros to the ventral surface of the post caval vein.

The size of the hypertrophied gonads apparently showed no important relation to the age at which the birds were operated or the time subsequent to operation at which they were examined. It seems probable that these gonads have attained their maximum size prior to 100 days post-ovariectomy, since those birds that were sacrificed at this time showed as great an hypertrophy as those that were sacrificed much later.

**Microscopic Examination:**

**General Considerations:** Twenty-five specimens were sectioned and histologically examined. This included some of the best developed compensatory gonads as well as those which showed no or very little growth. In all of the hypertrophied right gonads, the most
outstanding components were the cords of epithelial (medullary) cells (figs. 23 and 24). The fibrous connective tissue found between the cords is also abundant and sometimes forms a definite tunica albugenia, underneath the surface peritoneal epithelium. In almost every case examined, masses of lymphoid tissue in varying amounts could be seen infiltrating the tissue of the gonad. Similarly, capillaries with blood cells also penetrate into the gonad. In texture, some of the gonads showed a loose spongy appearance while others were fairly compact. The texture may vary within the areas of a single gonad.

Peritoneal covering: All of the hypertrophied gonads were covered on their free surfaces by a thin coelomic epithelium which entered into the curves and depressions found on the surface of some of them. The epithelium is composed of a single layer of squamous cells. In none of the gonads thus far examined, was there evidence of a thickened epithelium or of any proliferation from it. In other words, there was no sign of a cortex or of an active germinal epithelium.

Cords: The epithelial tissues found in the hypertrophied gonads were arranged mostly in definite cords of various sizes and shapes. In section the cords may be spherical or elliptical in shape (figs. 23 and 24); they may be short, or they may be long and extend into several sections as straight or twisted rods. The diameter also varies, ranging from approximately 25 μ to 75 μ. Cytologically most of the cords found in the hypertrophied gonad are of uniform
type. The cells within the basement membrane surrounding the
cords are not arranged in any definite manner. The cytoplasmic
outline of each cell could be easily made out even though the cell
membranes are not distinct. The nuclei are spherical as a rule
but oval ones were also observed. The nuclei show two distinct
nucleoli in the center of the nucleus slightly apart from each
other. With respect to the nature of the cytoplasm two types of
cells could be recognized. The predominant type has a homogenous
granular cytoplasm while the less abundant type has a clear, more
vesicular, cytoplasm and appears to be undergoing fatty degenera-
tion or disintegration. The cords may be composed entirely of
cells of the first type or of the second type or a combination of
the two (fig. 24). Both these types of cells may also be seen in-
dividually in isolated condition.

A second type of cord was noticed in one of the hypertrophied
gonads (fig. 23). In two adjacent cords, the cells were arranged
in such a manner that all of them were resting on the basement
membrane with their nuclei close to the base. These nuclei were
slightly smaller than those of the cells of the previously de-
scribed cords. The cytoplasm of each cell extends all the way to
the center of the cord, hence, no definite lumen is visible. It
is homogeneous and granular but the density of the stain decreases
toward the center of the cord.

In none of the hypertrophied gonads histologically examined,
did we find a definite tubule. It is also significant to note
that no germ cells were noticed in any of them.

**Connective tissue stroma and tunica albuginea.** Encircling the cords and the isolated epithelial cells, is the connective tissue stroma. The amount of tissue present between the cords differs according to the density of the cords. When the cords are few in a particular area, the stroma is either composed of a loose vascular or a more dense fibrous connective tissue. In areas where the cords are crowded, only very thin strips of connective tissue were present.

Underneath the peritoneal lining encircling the cordal tissue, a fibrous connective tissue tunica albuginea is seen in most of the hypertrophied gonads (fig. 24). This tissue may be thin or comparatively thick and in places it may occur in large rounded bundles stretching across the outer surface of the gonad.

**Lymphatic and Hemopoietic tissue:** Almost without exception, masses of lymphoid tissue may be seen infiltrated into the hypertrophied gonad. These may occur as huge masses occupying the spaces of degenerated cords or as loose strands entering into the intercordal areas. Capillaries containing blood cells are also seen in the stroma. However, these are not so abundant as to permit us to say that the gonads are well vascularized.

**Pigments:** It is not uncommon to see melanin pigment granules in the stroma of the hypertrophied right gonad. These, when present, are more abundant in the peripheral areas of the gonad than elsewhere.
Right gonads of doubtful hypertrophy

Right gonads of doubtful hypertrophy, so-called because their size is no larger than that of the normal rudimentary gonad, show the same component tissue elements as the hypertrophied gonad. In such gonads cords are few in number and small in size (fig. 25), and sometimes they were absent, in which case the cordal tissue is represented by isolated cells. Connective tissue cells as well as lymphocytes are prevalent in such gonads. In a few cases, the whole gonad was infiltrated with massive amounts of lymphatic tissue.

Regeneration on the site of the left ovary

Most of our ovariectomies were completely successful in the sense that no regeneration whatsoever took place at the site of left gonad. In twenty-five specimens histologically examined, 6 also showed a variable amount of regeneration on the left side (fig. 22). In one of these there was only a narrow, small strip of tissue while in another almost the same size as that of an average hypertrophied right gonad was attained. The disparity in the size of these regenerated masses is no doubt controlled, to some extent by the amount of tissue remaining following the operation.

Histologically, all of these left regenerated masses appear to be testis-like in character and similar in all respects to those found on the right. They are composed of cords, connective tissue stroma, and all the other tissue elements found in the
right gonads.

**Effects of Ovariectomy on Accessory Organs of Reproduction**

The accessory sex organs considered here are the left and right oviducts and the Wolffian ducts.

**Left Oviduct:** In almost all the cases of ovariectomy, regardless of the degree of hypertrophy of the right gonad, the left oviduct never revealed hormonal stimulation. It remained in the juvenile condition. In comparing the measurements of the left oviduct on the days the birds were ovariectomized and at the time they were autopsied (See Table III and IV for comparisons) it is evident that the oviducts continued to grow for only a short time after the operation and then stopped. The average length of these oviducts in poulards is about 3 to 4 cm. With few exceptions, the oviducts were narrow straight tubes and not well vascularized. In the exceptional cases (363, 356, and 957) they were slightly coiled and showed better vascularization.

**Right Oviduct:** As in the case of normal females, a rudimentary right oviduct was found in all the poulards without exception. They occur as small stumps (4 to 6 mm in length) attached to the right side of the cloacal wall and, in size and shape, were similar to those of juvenile female birds. In normal adult females, this rudimentary oviduct undergoes a slight enlargement in length and breadth, apparently due to estrogenic stimulation. In none of our poulards, was such stimulation observed in the right oviduct.

**Left and Right Wolffian Ducts:** Left and right Wolffian ducts were
found in all our female quail at all ages (fig. 19). Similarly, persistence of these ducts was observed without exception in our poulards as thread-like structures extending from the mesonephric remnant to the cloaca (figs. 20 and 21). Most of them occurred as straight ducts with slight coiling midway between cranial and caudal ends while others were straight throughout their entire course. This slight coiling, however, was not peculiar to the Wolffian ducts of poulards, for such coiling was also noticed in normal females as well as in capons. In none of our poulards was there an inversion of the duct into a vas deference such as is found in normal males.

Effects on Secondary Sex Characters

Effects on Plumage:

The Japanese quail undergoes a series of feather changes before it dons the adult plumage. The sequence of these changes has been reported by previous workers and recently by Lyon (1962). According to this author, the young coturnix reveals three sets of plumages, the natal, the first juvenile and the second juvenile prior to the acquisition of the adult winter plumage. The first juvenile feathers may begin to appear by the second day after hatching, replacing the natal plumage, and by four weeks post-hatch, the first juvenile plumage is almost completely developed. The first feathers of the second juvenile plumage make their appearance by 2½ to 3 weeks, well before the first juvenile plumage has completed its development. This second set is completely
developed at approximately 7 to 8 weeks after hatching. It is while in this plumage that the birds become sexually mature hence, some investigators have preferred to call this the nuptial plumage. The first juvenile plumage is acquired by a complete post natal molt while the second juvenile is only a partial one. In other words, the first post-juvenile molt preceding the second juvenile plumage is a partial molt. During this molt, feathers on the ventral, humeral, femoral, spinal, caudal and alar tracts are shed, but feathers on the crural, inferior and capital tracts are retained until the following second juvenile molt. This second post-juvenile molt, which is a complete molt, is followed by the winter plumage. Adult coturnix have two plumages and two molts per year, a complete molt in the late summer or fall, resulting in the winter plumage and a partial molt of the head and throat in the spring, February to April or May, resulting in the summer plumage.

The characteristics of the different plumages is as follows (after Lyon, 1962):

First Juvenile Plumage: Bill light brownish olive; head, neck and back grayish buffy brown. Feathers of the neck and back with a thin, pale cream, shaft streak; throat and breast white to pale grayish cream. Breast of both sexes with blackish brown spots, but in addition upper breast and lower throat of male tinged with light rufous; feet pale olive chestnut (figs. 30 and 31).

Second Juvenile Plumage: Bill, dark brownish olive to black;
forehead, nape, and crown dark buffy brown except for light cream median and superciliary lines; neck tawny, and back tawny to very deep buffy brown. Feathers of both regions with a broad, cream colored shaft streak; wing coverts, medium buffy brown with tawny spots or blotches on outer web. Secondaries similar but blotches larger and broader; abdomen white and tinged with very pale tawny. Feathers on sides dark tawny with a white shaft streak near the tip of the feather; throat in male solid cinnamon to chestnut and breast pale to light tawny. Throat of female pale grayish cream with black malar line descending onto edge of throat. Breast pale grayish cream with black or blackish brown spots; feet pale olive chestnut (fig. 32 and 34).

Winter plumage: Similar to second juvenile plumage except for coloration of throat and breast. Throat of male usually white with black anchor or streak (fig. 33). Breast pale to medium tawny. Throat and breast of female usually similar to second juvenile plumage, but sometimes will be identical to throat and breast coloration of the male.

In our laboratory some of the males of the second juvenile plumage showed the black anchor or streak (mentogular band) of the winter plumage. Because of this there may be some doubt about the genetic purity of our stock. This problem will be investigated.

Summer or Nuptial plumage: Same as that of second juvenile plumage.

The sex dimorphic feathers: As is clear from the above description
the first juvenile feathers are practically identical in both sexes. However, in the second juvenile plumage, as well as in the adult plumage, the coloration of the throat and breast feathers differs in both sexes. The throat and chin of the male may be uniformly solid cinnamon to chestnut colored as is usual in the second juvenile and summer plumages or, as is often seen in winter plumages, a variation of characters may be seen such as, 1) buffish white with a black or blackish brown, central, wedge-shaped, stripe of varying width curving back on each side in a narrow line to the ear coverts (as the influks of an anchor); at the base of the throat, curving back to ear coverts, 2) feathers of central stripe tipped pale buff, 3) curved lines on sides of throat often ill-defined and sometimes absent, 4) sides of throat often more or less chestnut, 5) in some, whole chin and throat chestnut, in others, mostly buff.

The breast feathers are orange-buff to chestnut-buff in color (figs. 32 and 33).

In contrast, the throat and chin of the female are pale grayish cream (figs. 34 and 35), but in winter, during the inactive period, variations may occur with a tendency to resemble the male type. The breast feathers are buff to rufous buff, spotted at the distal sides with black or blackish-brown and with narrow whitish shaft streaks (fig. 35). In winter, an occasional female may present a breast coloration identical with that of the male.

Although the plumage of the hen occasionally resembles that of the
male in every respect, males apparently never acquire a plumage similar to that of the typical female.

Changes due to ovariectomy prior to the first juvenile plumage

Ovariectomy even as early as the second day after hatching does not in any way affect the first juvenile plumage (fig. 31). This plumage appeared and was then replaced by the second juvenile plumage in all our birds irrespective of whether they were ovariectomized or not. This might be expected since there is no sex dimorphism in the first juvenile plumage.

Ovariectomy prior to the appearance of second juvenile plumage

The second juvenile and the adult plumages, both winter and summer, on the other hand, are affected by the removal of the left ovary. In poulards, operated prior to the development of the second juvenile plumage, all the emerging breast feathers showed the typical buffy male character without any indication of the black dots that are seen in the normal female. Similarly, the throat also showed the uniform chestnut color and occasional median black stripe, or mentogular band as in the male (figs. 36 and 37), which is the neutral form since, as will be seen later, quail canons also show the male pattern of plumage.

Ovariectomy after the attainment of the second juvenile plumage

When the birds were operated after the assumption of the second juvenile plumage, the feathers did not change into the male type until the succeeding winter molt. However, feathers that were accidentally lost or purposely plucked were replaced by the
adult male type. When feathers of the breast were plucked on the
day of operation, the new emerging feathers were found to be
mostly male, i.e., the neutral type, but some of them, especially
those that were away from the median line of the breast, were seen
to be slightly spotted black, resembling those of the female. The
significance of this will be discussed later.

Reversion of male plumage to the female type

Breast feathers were plucked at definite intervals, beginning
at the time of ovariectomy, to determine changes in the emerging
feathers. Birds operated in April showed male type feathers when
plucked in the following months until July when a few of the
feathers in some of the birds showed a mixture of male and female
types. This shows that the plumage of these birds was beginning
to revert to the female type as early as two to three months after
ovariectomy. A good number of our ovariectomized birds sooner or
later showed plumage of a mixed character (figs. 38 and 39), while
a few continued to retain the male type plumage (see Table IV).

The dotted breast feathers may appear all over the upper
breast of the poulard as in complete reversion, or they may be
restricted to either side rather than the median line as in many
of the cases of partial reversion. Again the black to brownish
spots may appear on either half of each feather or they may be
only on one side. When they are only on one side, they are usu-
ally seen on the lateral half of the feather. When one of the two
dots is dark and the other lighter, the lighter one usually
occupies the medial half. The significance of this will be discussed.

**Effect of ovariectomy on the size and rate of growth of the feathers**

An attempt was made to determine the difference, if any, in the lengths of identical feathers of poulards, capons, and normal females and males. For this purpose, the left second and third primaries, second and third secondaries and the left and right main tail feathers were selected and measured in 8 birds of each group. The summarized results are given in Table V. It is evident from these measurements that a slight increase in feather lengths is detected in the operated birds.

Similarly, an attempt was made to determine if there were any differences in rate of growth between the feathers of any of the four groups of birds under consideration. The same sets of feathers viz: left second and third primaries and secondaries and the two main tail feathers were plucked at the same time in six birds of each group and the emerging feathers measured at definite intervals during their growth. The results are tabulated and shown in Table VI. It is seen that the slight increase in length noticed in the operated birds, in contrast to the normals, is evident early in their growth, that is to say, the growth rate is higher in the operated birds in the early stages of growth.

**Effect on cloacal gland**

In the normal male the dorsal cloacal wall protrudes markedly
during the breeding season because of the hypertrophied cloacal gland. The gland consists of a number of single layered, sac-like compartments, opening directly into the proctodium. Each sac is lined by a high columnar epithelium which is folded inward forming many primary and secondary folds. The glands are surrounded on the dorsal side by thick outer circular and inner longitudinal layers of muscles (fig. 26). These glands secrete copious quantities of a frothy white material. During the non-breeding season, the gland as well as its musculature is greatly reduced in size and inactive.

In the normal female, this structure is an incipient cloacal gland. Here the sacs of the gland are lined with a low columnar epithelium and possess few, if any, secondary folds. Often it is infiltrated with lymphatic tissue. The musculature also is very scanty and no secretory material is ejected from the gland.

In none of the ovariectomized birds did we see a functional hypertrophied cloacal gland such as is found in the breeding male. The size of the gland remained small and not much different in gross appearance from that of the normal female. On histological examination, the glands were found to be lined by a medium to high columnar epithelium without any secondary folds. Varying amounts of lymphatic tissue infiltrated the stroma sometimes occupying the whole section and leaving very little space for the reduced sacs of the gland (fig. 27). The musculature of the gland also was not affected showing little, if any, difference from that of the normal
female. After comparing these glands with those of quail capons, it was evident that they were apparently not stimulated by the hypertrophied right gonads.

**Effects on voice and behavior**

It is well known that a castrated male bird is on the whole negative in its sexual behavior. Removal of the left ovary also resulted in the assumption of neutral behavior in the quail. The hypertrophy of the right rudimentary gonad into a testis-like organ, did not bring forth any noticeable male behavior in quail poulards. The males, especially during the breeding season, are very pugnacious and will fight, sometimes fiercely, when placed together in the same cage. No such fighting behavior was noticed in our poulards. Similarly, none of the poulards showed any attraction toward other females and they did not attempt to tread when normal breeding females were introduced into their cage. In the company of breeding males, the poulards, even those showing signs of reversion to the female plumage, behaved like unwilling females, running away as much as possible and thus refusing to oblige.

As for the voice, it has been reported (Witherby, 1941) that the call of the male is a liquid "quic, quie-ic", usually repeated several times and heard at night as well as in daytime. The ordinary call of the female is a soft "peu, peu". In our laboratory poulards were sometimes heard responding to the call of other quail but we were unable to determine whether their response
Sounded more like that of a male or a female. One interesting observation was that, when the tap water was turned on near the cages, where these birds were kept, the males as well as the poulards always made lots of noise which all sounded very similar.

**Effect on body size and weight**

Sexual dimorphism in the size of coturnix as judged by body weight, becomes apparent between 6 to 8 weeks of age (fig. 1). The average weight of a dozen males in one of our experimental groups was 113 gm when 137 days old. The mean weight of a dozen females of the same group and age was 135 gm. This disparity in weight is apparently due to the large glandular oviduct and ovulating ovary of the laying female as well as the additional accumulation of body fat. The weight of the poulard is greater than that of the male but lower than the female. The average weight of 20 poulards at 137 days of age was 126 gm. The accumulation of body fat seems, here also, to be the chief reason for this increase.

**On Bilateral Orchiectomy**

Twenty birds were bilaterally orchiectomized between the ages of 6 and 40 days and were sacrificed beginning from 180 to 600 days post operation. All were found to have been completely castrated on post mortem, that is to say, we found no testis-like tissue either by regeneration on the gonad sites or by growth of remnants that might have been accidentally lost in body cavity during the surgical removal.
Accessory organs Our observations indicate that the accessory organs of the male are greatly reduced in size following castration. The vasa deferentia, which in the normal male are tortuous and have a perceptible diameter, are reduced to a thin straight duct throughout most of their course. Some of them were slightly coiled midway between cranial and caudal ends but this condition may not be significant since it was seen in both the normal female and the sinistrally ovariectomized poulard.

Secondary sex characters

Plumage The plumage of castrated males was no different from that of normal males. This would seem to indicate that testicular hormones have no influence on the character of the plumage in male Japanese quail. Castration, even before the assumption of the first juvenile plumage, had no effect either on the juvenile plumages or the adult winter or summer plumages. Each of these plumages were similar to that of the normal male (figs. 40 and 41). The feathers in some of our capons seem to be darker than those of the male. This excess pigmentation is not limited to the feathers alone since the bill as well as the legs are somewhat darker in capons than in normal males.

As in the poulards, there appears to be a slight irregularity in the time of the molt of capons; however, our data at present are not sufficient to draw any definite conclusions on this point.

Size and rate of growth of feathers As will be seen from Table V, the lengths of certain primaries, secondaries and main tail
feathers were measured in capons, poulards, and normal males and females. The average lengths of the respective feathers in the capons were found to be slightly longer than the normal males. As for the rate of growth of the feathers of the capons, it is on a par with that of the poulard; the slight difference noticeable in the lengths of feathers of operated birds over that of normal males and females was attained in the early period when growth rate of operated birds was higher. Following this early period, growth rates became uniform and remained so until the feathers had reached full size.

**Cloacal gland** In none of the castrated males did we find the protruding cloacal gland characteristic of the breeding male. Instead, these glands were always small and similar in size to those of the laying female. When sexually active males were castrated, the size of the cloacal gland gradually involuted until it reached a size similar to that of the female. Histologically, such glands are lined with low to high columnar cells. The glandular sacs were reduced in size and lacked the secondary and sometimes the primary folds so conspicuous in the active male cloacal gland. The musculature covering the gland has also undergone considerable regression. Masses of lymphoid tissue may be seen infiltrating the glandular tissue. Sometimes, as also is the case in certain poulards, the whole gland is filled with lymphoid tissue leaving little or no space for the degenerated glandular sacs.

**Voice and behavior** The capons without exception were neutral in
their behavior. They showed none of the fighting attitude of the breeding male. Some of our capons were occasionally seen picking one another but this could in no sense be regarded as fighting behavior. In fact, females and males, during the non-breeding period, as well as the poulards, showed this picking behavior. Our capons did not show an interest in the female and did not attempt to tread even when submissive breeding females were placed in their cages.

During the breeding period the normal male is very restless and does a great deal of vocalizing which, apparently, is the sex call of the male. No such behavior was observed in our capons who did some vocalizing, especially when disturbed or alarmed. Such sounds are also made by the female as well as the poulard and therefore, should perhaps not be regarded as having any sexual significance.

**Body Size**  The size of our capons as measured by weight, increased beyond the normal as a result of early castration. The average weight of 15 capons at 137 days of age was 128 gm. This was 15 gm higher than the average weight of normal males of the same age. An excess deposition of fat was obvious in all our capons and this fact may explain their greater weight.
Development of the ovary:

The development of the ovary in the Japanese quail, in most respects resembles that of the chick whose embryology is well known through the studies of many investigators. Despite the difference in the incubation period of these two species, viz., 21 days for the chick and 16 to 17 days for the quail, the extent of development at the time of hatching is more or less the same with respect to the gonads. The events that take place in 21 days in the chick, therefore, have to be completed in a fewer number of days in the quail. Consequently, one sees an earlier appearance of structures in the case of the quail. For example, in the chick, Swift (1914, 1915) and others agree that the primordial germ cells arrive in the gonad area by 3½ days of incubation, while in the quail we find that they appear in the presumptive germinal epithelium by 2 to 2½ days. Such an acceleration in contrast to the chick is also noticed in the development of the medullary cords, proliferation of cortical cords and other major events of later development. Development in the quail is also speeded up during the post-hatch period since they become sexually mature as early as 45 days, whereas sexual maturity occurs at 5 to 6 months in the brown Leghorn fowl.
**Primordial germ cells**

The primordial germ cells of the quail resemble those described in the chick by Swift (1914), in size, shape and other characteristics. According to him, the cytoplasmic attraction sphere serves as the best criterion for identification of the germ cells. This was found not to be the case in the quail. An attraction sphere is nevertheless present, but only as a rather indistinct structure. On the other hand, Goldsmith (1928) did not find the attraction sphere as prominent in the chick as described by Swift.

As to the origin of the germ cells and their role in the formation of the definitive oocyte there is a wide difference of opinion. The majority of workers such as Nussbaum (1901), Rubaschkin (1907), Swift (1914, 1915), Goldsmith (1928), Matsumotto (1932), Benoit (1950), Domm and Clawson (1962), and others, who worked on the early development of the gonad in the chick, believe that the primordial germ cells have an extragonadal origin. Swift (1915) and Goldsmith (1928) especially, have shown that it is these germ cells that later give rise to the definitive oocyte. Waldeyer (1870) and d'Hollander (1904) among the early workers, on the other hand, believed that the germ cells are derived from the germinal epithelium. Firket (1913, 1920) thought that these cells come from an extragonadal area in the chick, but that most of these undergo degeneration beginning at 15 days of incubation and are replaced by new sex cells.
derived from the germinal epithelium. This view is supported by an earlier finding of Dantschakoff (1908) and more recently by Essenberg and Garwacki (1938) who believe that the definitive oocytes are derived entirely from the germinal epithelium. Although we did not make a detailed study on the origin and migration of these cells, our somewhat limited observations lead us to conclude that in the quail, they also have an extragonadal origin for they are found in other areas of the embryo such as the entoderm, the space between entoderm and mesoderm, and in the dorsal mesentery, prior to their arrival in the gonad. Similarly, we found no evidence of a widespread degeneration of these cells as was reported by Firket (1914) in the chick, but instead, we were able to trace them all through their development up to transformation into definitive oocytes. In the left ovary, germ cells located in the medullary area degenerate and disappear as the whole tissue itself undergoes degenerative changes, while those in the cortical area undergo a period of rapid mitotic proliferation, between seven and ten days, following which they enter the first stages of meiosis. Beginning with the day of hatching, the definitive ovum surrounded by its follicle begins to fill with deutoplasm and this process continues until the egg is mature and the follicle ruptures. It is true that many oocytes degenerate and disappear before even getting a follicular envelope and some even after considerable growth. This appears to be the normal way of getting rid of the multitude of oocytes that fill the embryonic
gonad but it in no way proves a discontinuity in the germ line of the primordial germ cells.

Firket (1913, 1914), Swift (1915), Blocker (1933), Stanley and Witschi (1940), Clawson and Domm (1963), and others have observed that the germ cells collect preferentially in the left gonad, in two to five times greater numbers than in the right. Such a difference is noticed in the chick embryo as early as 96 hours of incubation. However, prior to this time they are rather evenly distributed. Our observations in the quail support this early asymmetry. Prior to 2½ to 3 days of incubation the thickness of the germinal epithelium and the number of incorporated germ cells were almost equal on left and right sides. After this, we observed a slight increase in the thickness of the germinal epithelium on the left gonad as well as in the number of germ cells located in it. However, this disparity was not observed in all embryos. Some showed a near uniformity on left and right sides in this respect. In the quail, as in the case of most birds, only the left ovary becomes functional while the right begins to undergo regression during early development. In the case of the male, both right and left testes develop. Therefore, in the absence of evidence to the contrary, it may be logical to assume that the embryos which show the greater asymmetry may be developing in the female direction and the others the male. A more extensive study on the distribution of the germ cells in the quail is necessary before any firm conclusions can be drawn.
There is a difference of opinion as to the cause of this differential germ cell distribution. Dantchakoff (1931) believes that an asymmetry in the arterial distribution of the young embryo is responsible for the difference in numbers on the two sides. Witschi (1935a) contradicts this view and puts forth the idea that it is due to a primary, hereditarily fixed, deficiency in the right cortical inductor, which, therefore, fails to attract as many germ cells. Our observations would make it seem logical to accept the latter view for if it is due to an arterial asymmetry, one would expect a disparity in the distribution of germ cells in all embryos irrespective of sex; if, on the other hand, the attraction by the left cortex or its absence in the right cortex, due to a congenital deficiency is the cause, the chances are that this disparity would be limited mostly to those embryos which are developing into the female sex. We observed a sexual difference in distribution of the germ cells in the early embryos of the quail, however, more work is needed to establish the cause of this disparity.

Formation of the medullary cords

Conflicting opinions have been given as to the origin of the primary sex cords. Semon (1887) maintains that they are outgrowths of the capsules of the Wolffian body. Witschi (1935a, 1960), and Stanley and Witschi (1940) believed that the medulla is a pseudo-segmentally arranged cord-like, down-growth from an undifferentiated mesonephric "blastema" which is distinct from the
coelomic epithelium. Blocker (1933) had a similar view proposing a mesenchymal blastema origin of the medulla in *Passer domesticus*. However, the majority of workers such as Hoffman (1892), d'Hollander (1904), Firket (1914), Swift (1915, 1916), Benoit (1924, 1951), Goldsmith (1928), Brode (1928), Essenberg and Garwacki (1938), Willer (1939), and others, believe that in birds, the medullary cords are formed by ingrowths of cells from localized areas of the germinal epithelium (first proliferation). Our own observations in quail embryos strongly support this majority view. Bud-like projections on the inner surface of the germinal epithelium were seen at 4 days and by the 5th, proliferation was very active. Epithelial cords extending from the germinal epithelium and pushing into the mesenchymal blastema were very clearly observed during this period. We, therefore, conclude that in the quail embryo the medullary cords arise from the germinal epithelium.

**Fate of the medullary cords**

Firket (1914) thought that the primary sex cords degenerate completely in the female chick. In the male, of course, it is these medullary cords that give rise to the seminiferous tubules. More recently, (Brode, 1928; Willier, 1939), it was shown that the medullary cords also persist in the female after transforming into one of the following structures, distended tubules which may temporarily contain germ cells, clusters or cords of clear or 'fat laden' cells, isolated medullary cord cells, and isolated
primordial germ cells which, after a time, completely disappear.

In the quail, we see a similar transformation or degeneration of the medulla of the left and right female gonad. As in the chick, the bulk of the medullary tissue disappears but, nevertheless, small amounts persist throughout the life of the bird.

It is interesting to note that the transformation of the medullary cells, into 'fat laden' cells, and the regression of the right ovary, as well as the right oviduct, begins more or less at the same time. In the quail the 'fat laden' type of cell is visible in the medulla of both left and right gonads beginning on the 8th day of incubation and is abundant by the 9th. The right gonad as well as the right Mullerian duct also begins to regress by the 8th day. There has been much speculation regarding the cause of regression of the right oviduct in the female. Groenendijk - Huibers (1962) supports the idea that in the chick it is the male hormone which inhibits development of the right Mullerian duct. This would imply that the ovarian medulla of the embryo secretes a masculinizing hormone. The cells that produce this hormone, if there is one as suggested by the above author, and others, are not indicated. Looking at the morphology of the medulla at this stage one would expect either the medullary or the 'fat laden' cells to be the source of such a hormone. A cytological or histochemical approach should yield information on this point.
Cortex

At the end of the first proliferation, which occurs at about \(5\frac{1}{2}\) to 6 days in the quail, the germinal epithelium of the left gonad was found to be 3 to 5 cells thick while in the right, it was thinned out into a single layer in all cases observed. At the time the germinal epithelium of the left ovary began to proliferate the cortical cords, beginning on the 6th day, no such activity was noticed in the germinal epithelium of the right gonad. Later, either during incubation or after hatching we found no indication of a secondary proliferation or of the existence of cortical tissue in the right gonad. This does not agree with reported observations in some other birds. Brode (1928), who made a careful and detailed investigation on the right gonad of the chick from the time of sex differentiation to the adult stage, found some cortical tissue in the right gonad in 39% of the cases. Blocker (1933) also reported that in the right gonad of the female *Passer domesticus*, the cortex is developed only to a very slight extent or not at all. Similarly, Lewis (1946) reported that in the white Pekin duck,

"by the 10th day of incubation, the right ovary is covered with a single layer of epithelium which contains scattered primordial germ cells and, in some cases, a few large cortical cords that push out into the filmy area between the epithelium and the underlying medullary position".

The complete absence of cortical tissue in the right gonad of coturnix quail is significant and, as will be discussed later, it is no doubt because of this that all the hypertrophied gonads
in our ovariectomized birds appear to be entirely testis-like. Why there is no formation of cortex in any of the right gonads of female quail, while there is a sporadic development of cortex in the chick and in a number of other birds, is not known. We may conclude that in the quail, the genetic and/or hormonal inhibitory control of cortical development in the right gonad is complete, whereas in those forms where cortex occurs it is probably not.

**Interstitial cells of the ovary:**

The thecal wall of the ovarian follicle and the stroma of the ovaries of young and adult quail contains conspicuous cells, scattered singly or in small islets, which have a large vesicular cytoplasm and are sharply defined from the surrounding tissue. Such cells in the chick have been designated by various names, such as, "Interstitial cells" (Firket, 1914), "luteal cells" (Boring and Pearl, 1917), and "clear islet cells" (Nonindez, 1922). Boring and Pearl (1917) regarded these cells as true, secretory cells strictly homologous with the interstitial cells of the cow. Firket (1914) considered the "fat laden" cells of the medulla and the interstitial cells of the ovary as identical, but he claimed that they have a dual origin. The "fat laden" cells of the medulla are derived by a transformation of the cordal cells while the interstitial cells come from the connective tissue elements of the ovarian stroma. Nonindez (1922) and Fell (1923), who described the cytological details of interstitial cells, maintained that in the adult, these cells originated not from the connective tissue,
but from the epithelial cells derived from the original medullary cells. Benoit (1926) also concluded that they arise exclusively from the epithelial elements. Our observations, as to the origin of the interstitial cells in the quail, agree with the idea of an epithelial origin but cast some doubt on the idea that the precursors of the interstitial cells are derived from the original medullary cells or the epithelial cells of the first proliferation.

During the last days of incubation and after hatching, epithelial cells are liberated from the germinal epithelium which contribute to the stroma of the ovary. It was not possible, from our observations, to determine whether these secondary epithelial cells, or the original medullary cord cells that migrated into the cortical area, actually gave rise to the interstitial cells of the ovary. Until some histochemical or other method is found by which these cells of primary and secondary proliferation can be consistently and unequivocally identified the origin of the interstitial cells from either of these groups may not be known.

Ovarian asymmetry

The failure of the right gonad to develop into an ovary is a widespread phenomenon among birds. In the majority this gonad remains as a rudimentary structure. It is missing in strigidae (Stanley and Witschi, 1940). However, this is not the rule in all birds; Chappellier (1913) noticed the occurrence of a right ovary in some 44 species of birds belonging to 10 different orders. Domm (1939), and Stanley and Witschi (1940) also showed that in hawks
varying degrees of development of the right ovary takes place. Thus one can see a species variation in the degree of development of the right ovary.

In the quail, we have also noticed an individual variation in the amount of tissue that composes the right gonad. Brode (1928) observed such a difference in the chick. This individual variation, though small in magnitude, is nevertheless important, for as will be shown later, the extent of hypertrophy of the right gonad may depend, at least in part, on the amount of tissue present at the time of operation. Various theories have been proposed to account for this ovarian asymmetry in birds, a discussion of which is not called for here.

Gonadectomy:

Right gonad. Hypertrophy of the rudimentary right gonad occurred in the majority of our cases following sinistral ovariectomy. The question naturally arises as to why this should be so. The answer is not clearly understood despite the brilliant and repeated efforts of many investigators over the past four decades working on the domestic fowl and other birds where hypertrophy of this gonad also occurs. Since the mere removal of the left ovary results in hypertrophy of the right gonad, it is easy to infer that the left ovary is the inhibitory agent, but opinions differ as to what specific hormones or other influences of the left ovary bring this about. Kornfeld (1953, 1958) and Kornfeld and Nalbandov (1954) did extensive work on endocrine influences on the
development of the rudimentary right gonad of the fowl. By the administration of exogenous estrogen, and to a lesser extent androgen, it was possible for them to inhibit hypertrophy of the right gonad in ovariectomized fowl. Taber et al (1958) working on the same problem, also showed that estrogen and androgen had an inhibitory effect on the rudimentary right gonad. However, in all these cases the inhibition was only manifested in the medullary tissue. This led Gardner and Taber (1963) to conclude that the inhibition of the right gonad (both medulla and cortex) by the left ovary in normal birds must be affected not by the steroid-like estrogen and androgen but by some other substance secreted by the ovary. In fact, according to them they obtained a statistically significant inhibition of the right gonad following the administration of extracts from acetone dried ovaries containing no detectable steroids. The results of Kornfeld (1960), who induced proliferation of the rudimentary gonad in intact fowl by an anti-estrogenic agent (17α-ethyl-19 Nortestosterone), are baffling in the light of this evidence. These conflicting reports simply show that the mechanism by which the left ovary inhibits the right is not yet clearly understood and our findings in the quail shed no light on this problem. However, our observations help to prove one thing, and that is that removal of the left ovary in the quail does not always result in hypertrophy of the rudimentary right gonad an observation made earlier by Domm (1939) in a number of other birds.
In our experiments we observed hypertrophy of the right gonad in only about 80% of the cases, the rest showed practically no hypertrophy although some of their components appeared to be stimulated. Why this disparity? We may give the following seemingly plausible reasons. It could be assumed that there was actually hypertrophy in all our cases, but that in some, the hypertrophied gonad underwent a secondary regression. Gray (1930), studying some of the gonads from Domm's (1927) series, noticed such a secondary regression in some of the hypertrophied gonads of the brown Leghorn fowl; however, in none of these cases was the regression of such an extent that the hypertrophy completely disappeared. We do not believe that such a secondary regression is the likely cause of the absence of hypertrophy in some 20% of our poulards, for we noticed equally good hypertrophy in some of the old as well as young poulards, and cases of old as well as young which did not seem to show any hypertrophy. We feel that the possible answer to the differential hypertrophy lies in two factors; 1) the amount of tissue in the gonad at the time of ovariec-
tomy, and 2) the potential of the cells present to become re-
activated and undergo hypertrophy. The degree of hypertrophy and its relation to the amount of tissue initially present was noted in the domestic fowl by Domm (1927) and Gray (1930). We noticed an individual variation in the size and composition of the rudi-
mentary right gonad of the quail and this could have a bearing on the ultimate variation in the degree of hypertrophy observed.
This argument itself will not, however, completely solve the problem of the absence of hypertrophy in some of the cases, for in these at least a small amount of tissue was noticed on the right side, and one could argue that no matter how much or little tissue was present at the time of operation, it should have shown some hypertrophy. While it is practically impossible to prove that there was no hypertrophy, the small amount of tissue found in some of the gonads would be a priori evidence that no hypertrophy had occurred. This could mean that some of the rudimentary right gonads have lost the capacity to hypertrophy. Therefore, it would seem that not only the amount of tissue but also its capacity to become reactivated, in the absence of the inhibitory influence of the left ovary, are factors responsible for the degree of hypertrophy observed in the rudimentary right gonad of sinistrally ovariectomized birds. When a comparison is made between the quail and the brown Leghorn fowl, one may readily conclude that this regenerative capacity is much lower in the quail and is in fact, sometimes, even lacking.

This increasing loss of potentiality is also evident from our study on the histology of the hypertrophied gonad. In the chick, Gray (1930) described the development of the medullary cords and their transformation into tubules and he identified different types according to their stage of development. In the quail, none of the hypertrophied right gonads studied histologically showed any tubules. Only cords were present and these were mainly of the
first type mentioned by Gray in the chicken, although we found two isolated cases of Type B cords in one gonad. Some of the less hypertrophied gonads revealed very few, if any, cords and these were occasionally represented only by small isolated islets of epithelial cells. Hence, we see that there was very little differentiation of the epithelial cells and in none did they reach the stage of tubule formation. This result can not be due to a lack of time, since in the chicken the full transformation of cords into tubules took place within 5 to 6 weeks after ovariectomy (Gray, 1930). Many of our poulters were observed considerably beyond this period. Therefore, it is highly probable that the only answer for the lack of complete differentiation into tubules in the quail is a loss of the potentiality of the cord cells to develop and differentiate.

Thus, we may conclude that the development and differentiation of the rudimentary right gonad in these experiments depends not only on the removal of the left ovary, and thereby its inhibitory influence, but also on the amount of tissue present in the rudiment at the time of ovariectomy and its potential to hypertrophy.

If there is no tubule formation, one could naturally not expect to find spermatogenesis in the hypertrophied right gonad. Not only was there no spermatogenesis, but we saw no germ cells either in any of the gonads. This was to be expected since the germ cells were seen to disappear from the rudimentary right gonad
during the first three to four days after hatching. Even though some of our poulards were ovariectomized at two to four days of age, we found no evidence of spermatogenesis when they were sacrificed. Apparently, the germ cells had disappeared before the effects of ovariectomy could influence their further differentiation.

Another important finding concerning the hypertrophied gonad, is the complete absence of cortical or ovarian elements in any of the gonads studied. This was not unexpected, since no cortical tissue was found in any of the normal rudimentary right gonads of the embryos studied.

In cases where regeneration was observed on the site of the left ovary, the tissues were found to be testis-like showing all the structural characteristics of the hypertrophied right gonad. This indicates that the medulla of the left ovary also has the potentiality of developing into testis-like tissue. The absence of any ovarian tissue in the regenerated left gonad, apparently indicates that all cortical tissue was removed at the time of operation.

As to the functional activity of these hypertrophied gonads, we have no conclusive evidence that they produce any appreciable amount of male hormone as indicated by effects on either behavior, Wolffian ducts, or the cloacal gland. It was reported by Domm (1927), and others that following removal of the left ovary in the domestic fowl, the rudiments of the Wolffian ducts undergo growth
and differentiate into diminutive vasa deferentia. The reason given for this growth, was that it was the effect of male hormone produced by the hypertrophied right gonad. That the male hormone is necessary for the full development of the vas deferens in the normal male bird is a well established fact. In none of our poulards did we find a hormone stimulated convoluted Wolffian duct. These were usually thin, thread-like, straight ducts which only occasionally revealed a slight coiling midway between cranial and caudal ends. This type of coiling was also noticed in laying females as well as capons, which fact would indicate that when it occurs in poulards it is not necessarily brought about by androgenic hormones secreted by the hypertrophied gonad.

The lack of any appreciable amount of male hormone is also revealed by the failure of the cloacal gland of poulards to develop and secrete the white frothy fluid so prominent in normal breeding males. Nagra et al (1959) castrated males of the Japanese quail and observed that these glands had undergone regression in the capons. The administration of testosterone-cyclopentyl propionate in his castrates caused hypertrophy of the glands and the surrounding musculature as well as the appearance of the secretory material. Our castration experiments also showed that these glands never develop in the absence of the testes. When the cloacal glands of poulards and capons were compared, we found no appreciable difference in size or histological structure. Similarly, a comparison of these glands in poulards having an
hypertrophied right gonad and those showing very little, if any, hypertrophy, revealed no noticeable difference. This indicates that the hypertrophied testis-like gonads either did not secrete the hormone necessary for growth of the cloacal gland or, if they did secrete some hormone, which we believe more likely, the amount was below the threshold required for stimulation of the gland.

Castration of male coturnix did not have an effect on plumage and, in fact, there was no difference in the plumage of normal males and capons. This agrees with the observation in domestic fowl (Goodale 1913, Domm 1927, and others). Because of this fact, it is generally assumed that the cock plumage is the neutral form in these birds. When young quail were sinistrally ovariectomized, prior to the arrival of the first juvenile plumage, there was no change in the appearance or character of this plumage in the poulard. This indicates that the first juvenile plumage is in no way influenced by the secretions of the left ovary. However, all subsequent plumages, such as the second juvenile, and the adult winter and summer plumages, were affected by sinistral ovariectomy in that they all showed the male or neutral type of feathers instead of the female type. Thus, we see that the sex dimorphic female feathers in the quail are controlled by the left ovary, that is, the female feather in these plumages is the hormone controlled variant as in the domestic fowl (Domm 1927).

Domm (1927) described in detail the changes in the dimorphic feathers subsequent to sinistral ovariectomy in the brown Leghorn
fowl. He noticed that following the operation, all poulards don the male plumage. Later, many of them revert to a mixture of male and female feathers and ultimately the majority of them become completely female feathered. The appearance of female feathers in the poulard was attributed to female hormone secreted by the hypertrophied right gonad.

We also see a similar condition in the quail. Some of the poulards began to show the spotted breast feathers of the female as early as two to three months after the operation. If the appearance of black to brownish dots in the breast feather is directly related to the female hormone, then this reversion of certain of the feathers in the poulard would suggest that the right gonad in such cases produces female hormone. We have some direct proof to the effect that the colored dots in female feathers are indeed under the control of the female hormone. Ade Agostini (1936), by injecting follicular hormone (Serono's concentrated Oestrolase) into males of *Coturnix coturnix coturnix*, a sister race of the Japanese quail, produced the characteristic female spottiness in the upper breast feathers and the replacement of the mento-gular band of the male by the white feathers of the female throat. Hence, until such time as the observations of Agostini are disproved, or some other hormone has been shown to produce the same effect, we may conclude that the right gonad in the Japanese quail poulard also produces female hormone.

Ade Agostini (1936) also noticed that different feathers on
the breast showed different reactions to the follicular hormone. In some, the black dot was seen on both sides while in others it appeared only on one side. As described in detail, we also noticed this differential distribution of the colored dots. In reverted poulards, the spotted feathers were more prevalent on either side than in the median area of the upper breast. Again we noticed that when there was only one dot on a feather, it was usually on the lateral rather than the medial half. This phenomenon can be explained by applying the principle of differential sensitivity or thresholds of the feathers in different areas of the skin to hormones, as postulated by Lillie and Juhn (1932). If this principle is also true for the Japanese quail then we may postulate that the lateral half of the breast area is more sensitive to female hormone than the median area and the throat less sensitive than the breast for in many poulards the breast showed a mixed pattern, while the throat still showed the neutral character.

Since we found no ovarian tissue in any of the right gonads of our poulards, the source of the estrogentic hormone responsible for feminization of feathers has to be looked for among the cells of the hypertrophied medullary tissue. Gray (1930) suggested that in the reverted brown Leghorn poulard, the female hormone is produced by cords derived from a second proliferation of the germinal epithelium covering the hypertrophied right gonad. As for the male hormone, he believed that it was secreted by the medullary
cords of the first proliferation however, he was not able to distinguish these two sets of cords histologically. Our observations on the hypertrophied gonads of the quail, neither support nor disprove this claim however, we question Gray’s observation that cords of a second proliferation are formed and that these are the source of the female hormone. In the hypertrophied gonads of the quail, there was no indication of a second proliferation, nor of a reactivated germinal epithelium, which would indicate that there was or would be such a proliferation. In the light of our observations, we have to rule out the cords of second proliferation as the source of female hormone in quail poulards. Besides, the cords of first proliferation, to which is ascribed the source of the male hormone by Gray, the other probable element in the hypertrophied gonad to which might be ascribed a secretory function, is the 'fat laden' cell. Boring and Morgan (1918) and Nonindez (1922) implicated these cells as the source of female hormone in the Sebright bantam cock which is normally hen feathered. Even though we have this supporting evidence, one should refrain from ascribing to the 'fat laden' cell the source of the female hormone in the quail, until a reliable cytological or histochemical method is devised whereby one may detect the cells responsible for synthesis of the estrogenic hormone.

The presence of an estrogenic hormone in poulards may also be detected by its influence on the oviducts. The effect of estrogenic hormone on the development and maturation of the left oviduct
is well established (Domm and Gustovson 1929, Juhn and Gustovson 1930, Kar 1947, Brant and Nalbandov 1956, and others). It has also been shown in the chick, that subsequent to early sinistral ovariectomy, the left oviduct remains juvenile until such time as the right hypertrophied gonad begins to secrete sufficient amounts of estrogenic hormone to effect its development (Domm 1927). Except for three cases (No. 957, 356 and 363) the left oviducts of our poulards did not show any appreciable evidence of hormone stimulation even though some of them showed the spotted female feathers in the upper breast. Thus, it would appear that the threshold of the left oviduct for hormone stimulation is higher than that of the breast feathers. This is in line with the findings in the domestic fowl and other birds. In three cases which showed some coiling and greater vascularization of the left oviduct, poulard 957 should be eliminated since its oviduct was already coiled at the time of ovariectomy which was performed on the 35th day. In fact, a comparison with the oviducts of 35 day old normal females shows that there actually had been a slight regression in the oviduct of this poulard. Poulards Nos. 356 and 363 were operated when 14 and 16 days old, respectively, and their oviducts definitely showed some growth in size and vascularization, suggesting a possible estrogenic hormone stimulation. That these poulards had some spotted female feathers on their breasts at the time of autopsy, is additional support for the assumption that estrogenic hormone had been secreted. Both poulards had fairly large
hypertrophied gonads.

As stated earlier, the right oviduct is a rudimentary structure in the adult quail but it has been found to be somewhat enlarged in mature laying females in which left oviducts always show pronounced ovarian hormone stimulation. In none of our poulards did we detect hormone stimulated growth in the right oviduct even in those cases which showed growth of the left oviduct. This could mean that they require more female hormone than is being secreted in these poulards.

Based on his findings on the control mechanism of feathering in Finches, Witschi (1960) suggested that here as well as in the domestic fowl, the male or the so-called neutral plumage, is controlled by the pituitary leuteinizing hormone (LH). He argues that if the chicken hypophysis has the tendency of releasing LH in sufficient amounts throughout the year, which he thinks it does, to produce cock feathering, then henny plumage should form only whenever estrogen suppresses the LH output. Complete ovarietomy, by removing the source of estrogens, creates an unopposed LH condition with induction of cocky plumage. The validity of this speculation can be verified by hypophysectomy while keeping other conditions in the normal state. Hill and Parkes (1935) tried to accomplish this but their findings did not give a decisive answer. Until successful hypophysectomy experiments are performed and the other speculations of Witschi, such as the continuous supply of LH throughout the year, are experimentally proven, no serious support
can be given to the idea that the cock plumage is controlled by gonadotrophic LH in chick or quail.

A significant difference in the lengths of feathers in favor of the capons has been reported in the chicken (Zawdowsky 1922, Finlay 1925, Benoit 1929). Their data indicate that the testis exercises a certain degree of inhibition on the expression of male plumage. Our measurements on the feathers of quail capons, poulards, and normal males and females, do not show very significant differences, nevertheless a slight increase in favor of operated birds was observed. Therefore, the inhibitory effect of the male or other steroid hormones on the development of feathers in the quail, if any, is very little.

The Japanese quail shows a sexual dimorphism in body size as determined by weight. The adult females in our colony weighed about 20 to 30 grams more than the males. The extra weight is probably due, to a considerable degree, to the weight of the ovulating ovary and oviduct but the greater deposition of fat in the female must also be a factor. Both the castrated male and the sinistrally ovariectomized female showed significant increases in weight over normal males. The average weight of capons was seen to be about 128 grams at 137 days of age, while that of poulards of the same age was 126 grams. A greater deposition of fat in these birds as compared with normals appears to be the principal reason for their greater weight. Since normal males are smaller and not so heavy, it is easy to conclude that the testicular
hormone may be one of the factors responsible for their lower weight and size. If this is true and if any significance can be assigned to the difference in the weights of poulards and capons, it might be argued that this is another indication that the hypertrophied gonad secretes testicular hormone which has an effect on the weight of the poulard.

The capons as expected displayed the neutral behavior. They did not show the fighting or treading behavior characteristic of the male. Our poulards likewise did not display any of the behavior associated with the male, nor did they reveal the submissive attitude of the female. In fact, they behaved very much like capons. This would seem to indicate that if the hypertrophied right gonad did secrete male or female hormone, it was not produced in sufficient quantity to affect the behavior of the animal.
VI SUMMARY AND CONCLUSIONS

This investigation was concerned with the development of the gonads and the effects of sinistral ovariecotmy in the female and bilateral orchietomy in the male Japanese quail.

A. Development of the gonads

1. The incubation period was found to be 16 to 17 days at 100°F.
2. The primordial germ cells have an extragonadal origin. They began to appear in the gonad at about 2 to 2½ days of incubation.
3. An asymmetry in the number of germ cells was seen in most embryos beginning at 3 days of incubation with a preponderance in the left gonad.
4. Proliferation of the medullary cords from the germinal epithelium occurred between 4 and 5½ days. The mesenchymal elements occupied the intercordal area, as well as the area underlying the epithelium, to form the primary tunica albuginea.
5. Cortical cords began to proliferate from the epithelium of the left ovary on 6th day of incubation. Proliferation was active in the succeeding days at which time the germ cells underwent active multiplication. The right gonad revealed neither cortical cords nor cortex.
6. The right gonad began to involute around the 8th day when the
medullary cords either became luminated and distended or broke up into isolated or small groups of cells. Some of these cells transformed into 'fat laden' cells. A similar change was observed in the medulla of the left ovary.

7. Oogonia began to show meiotic changes as early as 11th day of incubation and oocytes were encircled by follicle cells beginning on the day of hatching. Ovulation was observed as early as 45 days post-hatch. Large numbers of 'interstitial cells', differentiated from the epithelial cells, appeared in the inter-follicular tissue of the ovary subsequent to hatching.

8. The right gonad reached its minimum size by 7 to 10 days after hatching. In adults it was composed of loose epithelial cells with no or very few 'fat laden' cells supported by fibrous connective tissue. Blood cells and lymphocytes were also seen. By 3 to 4 days after hatching all germ cells had disappeared from the right gonad or could no longer be recognized.

B. Gonadectomy

1) Sinistral ovariecetomy

9. Forty-nine females were sinistrally ovariecetomized at ages ranging from 2 to 35 days.

10. Sinistral ovariecetomy resulted in some hypertrophy of the rudimentary right gonad in about 80% of the cases. Such gonads were composed of cords of epithelial origin, 'fat
laden' cells, intercordal connective tissue, masses of lymphatic tissue and some blood vessels. The covering epithelium was thin and showed no indications of a secondary proliferation or cortex.

11. In six cases of ovariectomy regenerated testis-like masses devoid of cortex were observed on the site of the left ovary all of which resembled the hypertrophied right gonad.

12. The Wolffian ducts of poulards did not exhibit any appreciable hormonal stimulation following hypertrophy of the right gonad and Mullerian ducts showed some growth in only two cases.

13. The first juvenile plumage was not affected following ovariectomy but subsequent plumages changed to the male type. A slight increase in length was observed in 2nd and 3rd primaries and secondaries as well as in the main tail feathers which became apparent early in the growth of these feathers. After a variable period, some poulards reacquired female type feathers on lower neck and upper breast.

14. Poulards were neutral in behavior and revealed no hypertrophy of the cloacal gland. Their weights averaged 126 grams at 137 days of age which was midway between that of normal males and females of the same age.
2) **Bilateral orchietomy**

15. Twenty males were bilateraly orchietomized at ages ranging from 6 to 40 days.

16. The Wolffian ducts of castrated males remained straight, thin and thread like.

17. Orchietomy caused no noticeable change in the feather pattern showing that the male plumage is the neutral form.

18. Capons displayed a neutral sex behavior and their cloacal glands were small and inactive. The weight of adult capons averaged about 15 grams more than that of normal males which, as in poulards, appeared to be primarily due to excess deposition of fat.

C. **Conclusions**

19. The apparent inability of any cortical tissue to develop in the right gonad of the female embryo is assumed to be due to a complete inhibitory control by genetic and/or hormonal factors.

20. The absence of any appreciable hypertrophy of the right gonad in some 20% of our poulards and the varying degrees of hypertrophy in the rest of the cases is tentatively attributed to the amount of tissue present and its growth or reactivation potential at the time of ovarietomy. The failure of the cords of hypertrophied gonads to form tubules is also tentatively ascribed to a loss in reactivation potential.
21. The absence of cortical tissue in hypertrophied right gonads is ascribed to the absence of such tissue in the normal rudimentary right gonad at the time of ovariectomy.

22. The reappearance of female feathers in our poulards, and growth of the left oviduct in two of the cases in the absence of any recognizable cortical tissue is tentatively ascribed to the production of ovarian hormone by the 'fat laden' cells of the right gonad.

23. The absence of any noticeable stimulation in Wolffian ducts and cloacal glands as well as male behavior in poulards is attributed to an insufficient amount of male hormone rather than to its complete absence.
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TABLE I

SPECIMENS EXAMINED IN MICROSCOPIC STUDY OF GONADS

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TABLE III

MEASUREMENTS OF REPRODUCTIVE ORGANS IN POST EMBRYONIC PERIOD

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* slightly coiled midway between cranial and caudal ends
* coiled and better vascularized
+ length and breadth
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<tr>
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<td>236</td>
<td>4.0 x 0.9 / 2 x 0.8</td>
<td>30</td>
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<td>34</td>
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<tr>
<td>413</td>
<td>22</td>
<td>1-9-63</td>
<td>209</td>
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<td>209</td>
<td>3.4 x 1.0</td>
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<td>42</td>
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<td>mixed</td>
</tr>
<tr>
<td>453</td>
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<td>11-20-62</td>
<td>157</td>
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<td>38</td>
<td>6</td>
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<td>neutral</td>
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<td>mixed</td>
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<td>4</td>
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<td>10-3-62</td>
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<td>8-18-63</td>
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<td>42</td>
<td>4</td>
<td>* coiled</td>
<td>neutral</td>
</tr>
</tbody>
</table>

* slightly coiled midway between cranial and caudal ends
+ coiled and better vascularized
@ coiled and better vascularized

TABLE IV Contd.

DATA ON SINISTRALLY OVARIECTOMIZED BIRDS
### A. MEASUREMENTS ON THE LENGTH OF FEATHERS

<table>
<thead>
<tr>
<th>Type of Bird*</th>
<th>2nd Primaries</th>
<th>3rd Primaries</th>
<th>2nd Secondaries</th>
<th>3rd Secondaries</th>
<th>Main Tails L</th>
<th>Main Tails R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>8.32 cm</td>
<td>8.32 cm</td>
<td>5.86 cm</td>
<td>5.88 cm</td>
<td>4.45 cm</td>
<td>4.49 cm</td>
</tr>
<tr>
<td>Females</td>
<td>8.40 cm</td>
<td>8.50 cm</td>
<td>6.06 cm</td>
<td>6.06 cm</td>
<td>4.47 cm</td>
<td>4.45 cm</td>
</tr>
<tr>
<td>Capons</td>
<td>8.56 cm</td>
<td>8.60 cm</td>
<td>6.03 cm</td>
<td>6.01 cm</td>
<td>4.55 cm</td>
<td>4.53 cm</td>
</tr>
<tr>
<td>Poulards</td>
<td>8.52 cm</td>
<td>8.50 cm</td>
<td>5.95 cm</td>
<td>5.95 cm</td>
<td>4.51 cm</td>
<td>4.49 cm</td>
</tr>
</tbody>
</table>

*Feathers from eight birds of each group were measured & averaged.

### B. COMPARISON OF FEATHER LENGTH BETWEEN GROUPS

<table>
<thead>
<tr>
<th>Between groups</th>
<th>Primaries Mean</th>
<th>S.D.</th>
<th>P</th>
<th>Secondary Mean</th>
<th>S.D.</th>
<th>P</th>
<th>Main Tails Mean</th>
<th>S.D.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Female</td>
<td>8.32 ± 0.5</td>
<td>&lt;.05</td>
<td></td>
<td>5.87 ± 0.5</td>
<td>&lt;.01</td>
<td></td>
<td>4.47 ± 1.27</td>
<td>.1</td>
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<tr>
<td>Male Poulard</td>
<td>8.51 ± 0.48</td>
<td>&lt;.01</td>
<td></td>
<td>5.95 ± 0.76</td>
<td>&lt;.01</td>
<td></td>
<td>4.51 ± .55</td>
<td>.1</td>
<td></td>
</tr>
<tr>
<td>Female Poulard</td>
<td>8.45 ± 0.12</td>
<td>&lt;.01</td>
<td></td>
<td>6.06 ± 0.58</td>
<td>&lt;.001</td>
<td></td>
<td>4.46 ± .825</td>
<td>.1</td>
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<tr>
<td>Capon</td>
<td>8.58 ± 0.81</td>
<td>&lt;.01</td>
<td></td>
<td>6.02 ± 0.57</td>
<td>&lt;.05</td>
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<td>4.54 ± .49</td>
<td>.1</td>
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<tr>
<td>Poulard</td>
<td>8.51 ± 0.48</td>
<td>&lt;.01</td>
<td></td>
<td>5.95 ± 0.76</td>
<td>&lt;.01</td>
<td></td>
<td>4.54 ± .49</td>
<td>.1</td>
<td></td>
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</tbody>
</table>

* Significant, S.D. = Standard deviation, P = Probability
### TABLE V

**MEASUREMENTS ON THE GROWTH RATE OF FEATHERS**

<table>
<thead>
<tr>
<th>Type</th>
<th>Combined average of 2nd &amp; 3rd primaries length in cm</th>
<th>Combined average of 2nd &amp; 3rd secondaries length in cm</th>
<th>Combined average of left and right main tails length in cm</th>
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<tbody>
<tr>
<td></td>
<td>Days of growth</td>
<td>Days of growth</td>
<td>Days of growth</td>
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<tr>
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<td>11th 17th 23rd 35th</td>
<td>11th 17th 23rd 35th</td>
<td>11th 17th 23rd 35th</td>
</tr>
<tr>
<td>Males</td>
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<td></td>
</tr>
<tr>
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<td></td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.73 3.99 5.96 7.35 2.18 4.29 5.16 5.18 0.97 2.27 3.26 3.88</td>
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<td></td>
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<tr>
<td>Capons</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>2.19 4.68 6.60 7.50 2.39 4.57 5.25 5.28 0.92 2.10 3.27 4.18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pou-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lards</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.06 4.57 6.57 7.56 2.53 4.60 5.26 5.32 1.13 2.48 3.65 4.25</td>
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</tbody>
</table>

* Feathers from six birds in each group were measured and averaged.
Figure 1. Graph showing the post-embryonic growth in weight of males, females, capons and poulards.
Figure 2. Photomicrograph of a primordial germ cell (PGC) located between the ectoderm and mesoderm of a quail embryo of 28 hours incubation. Note the large size of the nucleus and the cytoplasm filled with lipid granules. X 2400

Figure 3. Cross section of a 2½ day old embryo showing the germinal epithelium (GE) with newly arrived primordial germ cells (PGC). X 225
Figure 4. Cross section through the left (L) and right (R) gonads of a 4 day old embryo. Note the preponderance of primordial germ cells (PGC) in the left gonad. X 225
MB. Mesenchymal blastema.

Figure 5. Cross section through the left gonad of a 5 day old embryo showing the ingrowth of the primary or medullary sex cords (MC) from the germinal epithelium (GE). X 550
Craso section through the left and right ovaries of a 6 day old embryo. Note the slight difference in the size of the left (L) and right (R) gonads. X 200

Figure 6. Cross section through the left and right ovaries of a 6 day old embryo. Note the slight difference in the size of the left (L) and right (R) gonads. X 200

Figure 7. Cross section through the peripheral portion of the left and right ovaries of a 6 day old embryo (same as in Fig. 6). Note the thin single layered germinal epithelium (GE) of the right gonad and the thick multilayered epithelium of the left gonad. The thick epithelium also shows small invaginations in places thus indicating the beginning proliferation of the secondary or cortical cords (CC). X 500

MC. Medullary cords.

MC

GE

CC

FIGURE 6

FIGURE 7
PLATE 5

Figure 8. Cross section of the left gonad of an 8 day old female embryo. Note the already separated cortical cords (CC) and the disintegrating medullary cords some of which show a central lumen. X 295

Figure 9. Cross section of the right gonad of an 8 day old female embryo. Note the absence of cortex and cortical cords; the germinal epithelium is very thin. Medullary cords (MC) are loosely arranged and many lacunae (L) and vacuoles (V) are seen in and around these cords. X 295
PLATE 6

Figure 10. Cross section of the left ovary of an 11 day old embryo showing a portion of the cortex and the underlying medullary tissue. Note the oocytes in synizesis (O) at the inner aspect of the cortex and islets of 'fat laden' cells (FLC) in the medulla. X 975

Figure 11. Cross section of the right gonad of an 12 day old female embryo. Note the thin germinal epithelium (GE). Also note the lacunae and vacuoles in the medulla and the disintegrating medullary cords. X 825

FLC. 'Fat Laden' cells.
Figure 12. Cross section through the right rudimentary gonad and a portion of the left ovary of a 14 day old embryo. Note the wide disparity in size between the rudimentary right gonad (RRG) and the left ovary (LO). X 225
PLATE 8

Figure 1a. Portion of the cortex of the left ovary of a newly hatched quail (17 days incubation). Note the oocyte (O) being enveloped by follicle cells (FC). X 940

Figure 1b. Cross section through the rudimentary right gonad of the above quail (Fig. 1a). Note the 'fat laden' cells (FLC) and other loose epithelial cells (EC). X 375
Figure 17. Cross section through the rudimentary right gonad (RRG) of a 70 day old quail. X 135

Figure 18. High power view of the gonad shown in figure 17. Note the loose epithelial cells (EC) under the thick outer fibrous theca (FT). X 720
Figure 19. The urinogenital system of a young adult female (100 days) showing the position of the rudimentary right gonad. X 25
OVD. Oviduct, LO. Left Ovary, RHG. Rudimentary right gonad, WD. Wolffian duct.

Figure 20. The urinogenital system of a sinistrally ovariectomized poultard (X3/5) showing prominent testis like right gonad. This bird had been sinistrally ovariectomized when 6 days old and was killed 400 days later. X 25
OVD. Oviduct, RHG. Hypertrophied right gonad, M. Mesonephros, WD. Wolffian duct.

Figure 21. The urinogenital system of sinistrally ovariectomized poultard (X4/5) which had been ovariectomized when 3 days old and killed 222 days later. X 25
AD. Adrenals, HLG. Hypertrophied left gonad, RHG. Hypertrophied right gonad, OVD. Oviduct, WD. Wolffian duct.
PLATE 12

Figure 22. Cross section through the left and right hypertrophied gonads of a sinistrally ovariectomized poult (440). This bird was ovariectomised when 22 days old and killed 155 days later. X 28
R. Right gonad, L. Left gonad.

Figure 23. Cross section through certain cords of the hypertrophied right gonad shown in figure 22. Note the type A and type B cords surrounded by connective tissue stroma. X 535
Figure 24. Cross section through the hypertrophied right gonad of a poultard (6363) which was sinistrally ovariectomized when 16 days old and killed 185 days later. Note the cords composed of epithelial cells (EC), 'fat laden' cells (FLC) and cords containing both these cells. Also note the fibrous tunica albuginea (TA) and infiltrated masses of lymphatic tissue (LT). X 210

Figure 25. Cross section through the right gonad of a poultard (6410) which had been sinistrally ovariectomized when 28 days old and killed 325 days later. This is one of the cases (approximately 20%) in which no or very little hypertrophy of the right gonad was noticed subsequent to the operation. X 550

EC. Epithelial cells, FLC. 'Fat laden' cells.
Figure 26. Cross section through the cloacal gland of an adult breeding male. Note the units of secretory glands and the heavy musculature overlying them. X 11

G. Gland, M. Musculature.

Figure 27. Cross section through the cloacal gland of a poultard (A458) which was sinistral ovarioctomized when 4 days old and killed 11.5 days later. Note the infiltration of lymphoid tissue into the area of the degenerated glands. The musculature is also feebly developed in contrast to the normal (Fig. 26). X 16
PLATE 15

Figure 28. Quail eggs (Coturnix coturnix japonica) to show their size and the variations in color pattern. X 0.5

Figure 29. One day old quail chick - note down plumage. X 0.5

Figure 30. Two week old chick (#356). The first juvenile plumage has appeared except on head and ventral side of the body. X 0.5

Figure 31. Poultard #356 (Fig. 30). Ten days after ovariectomy. This bird was sinistrally ovariectomized when 14 days old while the median area of the breast was still covered with down feathers (compare figure 30). Ovariectomy did not alter the normal development of the dotted feathers of the first juvenile plumage of the breast area. X 0.5
Figure 32. Normal male (120 days old) in 2nd juvenile or the summer plumage (both are identical). Note the uniform buffy breast feathers and the more or less uniform cinnamon colored throat. X 0.5

Figure 33. Normal male (180 days old) in winter plumage. Note the dark wide stripe under the throat. Such stripes frequently occur and are characteristic of the winter plumage. X 0.5

Figure 34. Normal female (120 days old) in second juvenile plumage. Note the pale grayish cream throat feathers with black malar line descending onto edge of throat. The breast feathers are grayish cream with black dots. X 0.5

Figure 35. Normal laying female (325 days old). The feathers are identical with those shown in figure 34 since there is no characteristic difference in the adult female plumage and the 2nd juvenile female plumage. However, note the comparatively prominent black dots on a wider area of the breast feathers. X 0.5
Figure 36. Poulard #404. This bird was sinistrally ovariec- tomized when 24 days old and the photograph was taken in March, 280 days after the operation. Note the male-type breast feathers and the uniform darkish throat feathers. X 0.5

Figure 37. Poulard #452. This bird was sinistrally ovariec- tomized when 22 days old and the photograph was taken in April, 303 days after the operation. The breast feathers are a uniform buff color as in poulard #404, (Fig. 36) but the throat shows the characteristic montogular stripe. This poulard had not reacquired any female feathers prior to this period. X 0.5

Figure 38. Poulard #374. This bird was sinistrally ovariec- tomized when 5 days old and the photograph was taken in July, 455 days after the operation. Note the dotted breast feathers an indication that these feathers have reverted. X 0.5

Figure 39. Poulard #450. This bird was sinistrally ovariec- tomized when 20 days old and the photograph was taken in July, 375 days after ovariectomy. Like #374 (Fig. 38) this also shows reversion of feathers in the breast area. The feathers under the throat, however, remain male like. X 0.5
PLATE 18

Figure 40. Capon #393. This bird was bilaterally orchiectomized when 18 days old and the photograph was taken in March, 276 days after the operation. Note the uniform buff colored breast feathers and the cinnamon colored throat feathers similar to those of a normal male. X 0.5

Figure 41. Capon #428. This bird was completely castrated when 32 days old and the photograph was taken in March, 310 days after the operation. The breast and throat feathers did not change as a result of the orchiectomy. Note the faint mentogular band under the throat. X 0.5
The dissertation submitted by Jose Vacco Kannankeril has been read and approved by five members of the faculty of the Graduate School.

The final copies have been examined by the director of the dissertation and the signature which appears below verifies the fact that any necessary changes have been incorporated, and that the dissertation is now given final approval with reference to content, form, and mechanical accuracy.

The dissertation is therefore accepted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy.

DATE May 25, 1964

Signature of Advisor