THE CONDOR

VOLUME 65 JULY-AUGUST, 1963 NUMBER 4

REPRODUCTION AND DEVELOPMENT OF YOUNG IN A POPULATION OF CALIFORNIA QUAIL

By VICTOR LEWIN

This study concerns the processes of reproduction in a population of California Quail (*Lophortyx californicus brunnescens*) from a restricted area in the upper reaches of Strawberry Canyon, Alameda County, California. During a three and one-half year period, from October, 1953, through March, 1957, a total of 485 quail were trapped in the study area, and in addition 74 chicks were artificially hatched and reared in captivity. Particular attention was directed to following the gross and histological variations in reproductive organs of adult male and female quail throughout the year. Additionally, an effort has been made to describe the growth and/or regression of various structures which serve as aging criteria for young quail.

The sequence of events during the breeding season was obtained by histological examination of adult gonads. Methods were then devised to enable the accurate prediction of these events by the gross examination of various reproductive structures in adult males and females and by accurate aging of young quail.

An attempt was made to present graphically in integrated form the known facts on the sequence and timing of behavioral, physiological, and morphological events in both adult and juvenal quail.

ACKNOWLEDGMENTS

The writer wishes to express his gratitude to Dr. A. Starker Leopold, for his guidance and encouragement in all phases of this study. I am grateful to Gene M. Christman for his excellent anatomical drawings. A. Starker Leopold, Oliver P. Pearson and Lewis W. Taylor read the manuscript and offered helpful suggestions. Richard Genelly donated 103 quail eggs which were incubated at the Yountville State Game Farm, under the direction of Ken Doty. Financial assistance during the terminal phases of this study was provided by the Martens Fund of the Museum of Vertebrate Zoology. Much support was derived from the Department of Zoology, particularly from the storeroom. I am especially grateful to Geraldine Lewin for her enthusiasm throughout the study and for her help with the compilation of the data.

THE STUDY AREA

The study area is located in the upper reaches of Strawberry Canyon, on the campus of the University of California in Berkeley. The specific trapping area lies along the fire road that parallels the 1200-foot contour line and approaches to within one-quarter of a mile of Grizzly Peak at the head of the canyon. Quail were taken from a strip 100 yards wide on each side of the fire road for a distance of one and one-half miles from where the road connects with Grizzly Peak Boulevard. This area belongs to the University of California and is closed to public use. There has been no grazing on the area for over 25 years.

The study area is steep, well drained, and has numerous small canyons all draining into Strawberry Creek. There is one large plantation of eucalyptus trees and many small groups of these trees are scattered throughout the area. The drier south-facing slopes support grass, principally wild oats (*Avena fatua*), and coyote brush (*Baccharis pilularis*). These species are replaced by poison oak (*Rhus diversiloba*), California laurel (*Umbellularia californica*), and live oak (*Quercus agrifolia*) in the deeper canyons. There are also scattered small plantations of Monterey pine (*Pinus radiata*).

The climate is mild, typical of the coast of central California. Frosts, hail or snow are infrequent. The average rainfall on Grizzly Peak is 20.2 inches, most of which (17.2 inches) falls between October and March. There is relatively little rain (2.8 inches) from April through June, and hardly any (0.2 inch) from July through September. Ocean fogs may occur at any time of the year but are most frequent during summer.

METHODS

Trapping.—Quail of all ages readily enter wire traps in all seasons of the year. The traps were designed after the standard quail trap of Stoddard (1931:443) and were constructed of galvanized one-inch hexagonal poultry netting. They were three feet square and one foot high with a wire cone entrance attached to one side and tapering to four inches in height toward the middle of the trap. No closing device was used at the end of this cone. Washers were wired to the corners of the trap so that it could be fastened to the ground with large nails. A six by six inch flap was cut in the top to facilitate removal of the birds.

The traps were left in the field at all times and as many as six were in use at one time. They were set almost constantly during the period of study and were visited just before dark, when the birds were removed and new bait was added. A commercial bird seed mixture was used as bait.

Treatment of birds.—The birds were either retained alive over night or dissected within an hour after capture. Total body weight was recorded to the nearest tenth of a gram and the right wing was pinned out to dry for molt analysis. The volume and contents of the crop were recorded if food other than trap seed was present. The lengths of one caecum and of the small intestine from the gizzard to the caecal junction were taken to the nearest half centimeter. The mid-section of the back with reproductive organs attached was preserved, along with the gastrointestinal tract and the bursa of Fabricius, in Bouin's picro-formol-acetic solution. After preservation, the length and width of the left testis was taken with dial calipers to the nearest 0.1 millimeter. The left testis was in all cases the larger one. A median section of the left testis was then removed for later microscopic analysis. The gross condition of the vas deferens was recorded and in some cases smears of its contents were made. The ovary was weighed, after preservation, to the nearest 0.01 gram and the greatest diameter of the largest ovarian follicle of the nonbreeding birds was recorded. In breeding females the greatest diameter of each of the developing ovarian follicles and the greatest width of each of the regressing postovulatory follicles were recorded to the nearest 0.1 millimeter. The entire oviduct of each female was weighed, and during the laying season the weight of shelled eggs and their condition was recorded either as "hard" or "soft," "pigmented" or "nonpigmented." The position of an egg in the oviduct was also noted.

All tissue prepared for histological examination was fixed in Bouin's picro-formol-acetic solution within five minutes after death. It was then dehydrated in dioxane, imbedded in paraffin, sectioned at 7 microns, stained progressively in either Delafield's or Harris's hemotoxylin, counter stained with eosin, and then mounted in balsam.

Terminology.—Because there are three age classes of birds recognizable during a short time following the breeding season, three terms must be used to denote age. The term juvenile refers to a bird until the completion of the postjuvenal molt, which according to Raitt (1961) occurs during the twenty-first week of life (by the end of the first week in December). The term immature refers to a bird from the time of completion of the postjuvenal molt until the completion of the first postnuptial molt. During this time, the distinguishing feathers are the buff colored upper primary coverts and the more pointed outer two juvenal primaries. After the postnuptial molt these juvenal feathers which have been retained over the first winter are molted and the bird is then called adult.

SEX AND AGE RATIOS

The seasonal distribution of the total sample of birds is presented in table 1. Following the terminology of Mayr (1939) the secondary sex ratio, or the proportion of each sex at hatching appears to be equal, as 36 juvenal males and 35 juvenal females

TABLE 1

SEX AND AGE RATIOS

		Spring Mar.–May		Summer June–Aug.		Fall Sept.–Nov.		Winter Dec.–Feb.	
		No. birds	Per cent pop.	No. birds	Per cent pop.	No. birds	Per cent pop.	No. birds	Per cent pop.
Adults	♂♂	37	26.2	20	14.8	13	21.0	31	21.1
	♀♀	29	20.6	12	8.9	11	17.7	26	17.7
Immatures	♂♂	42	29.8	18	13.3	....	....	46	31.3
	♀♀	33	23.4	14	10.4	....	....	44	29.9
Juveniles	♂♂	....	....	36	26.7	16	25.8	....	....
	♀♀	....	....	35	25.9	22	35.5	....	....
Totals		141	100	135	100	62	100	147	100

Sex ratio overall = 259 males : 226 females, or 111.4 males : 100 females (or 53.4 per cent males).

were trapped during the summer period. The fall sample shows some distortion of the sex ratio, containing 16 juvenal males and 22 juvenal females. This small sample suggests that during the first few months of life the males may suffer a higher degree of mortality than do the females, a situation previously noted by Genelly (MS), Williams (1957), and Raitt (MS). By winter the sex ratio has reversed and is slightly in favor of males. During this time 46 immature males and 44 females were taken. The tertiary sex ratio in quail, or the proportion of the sexes during adult life, is well established and is always in favor of the males. The sex ratio of all breeding quail (the spring and summer sample, exclusive of juveniles) was 117 males to 88 females, or 57.1 per cent males. The overall sex ratio of the total sample of 485 birds was 259 males to 226 females, or 53.4 per cent males.

MALE REPRODUCTIVE CYCLE

The timing and annual variations of the male cycle were studied and correlated with corresponding stages in the female cycle and with the yearly changes in climate. A group of 200 testes consisting of 82 from adults, 81 from immatures, and 37 from juveniles were used in this study. This sample covers every month of the year. Only the larger testis, the left in all cases, was used. (See fig. 1 for male reproductive tract in breeding

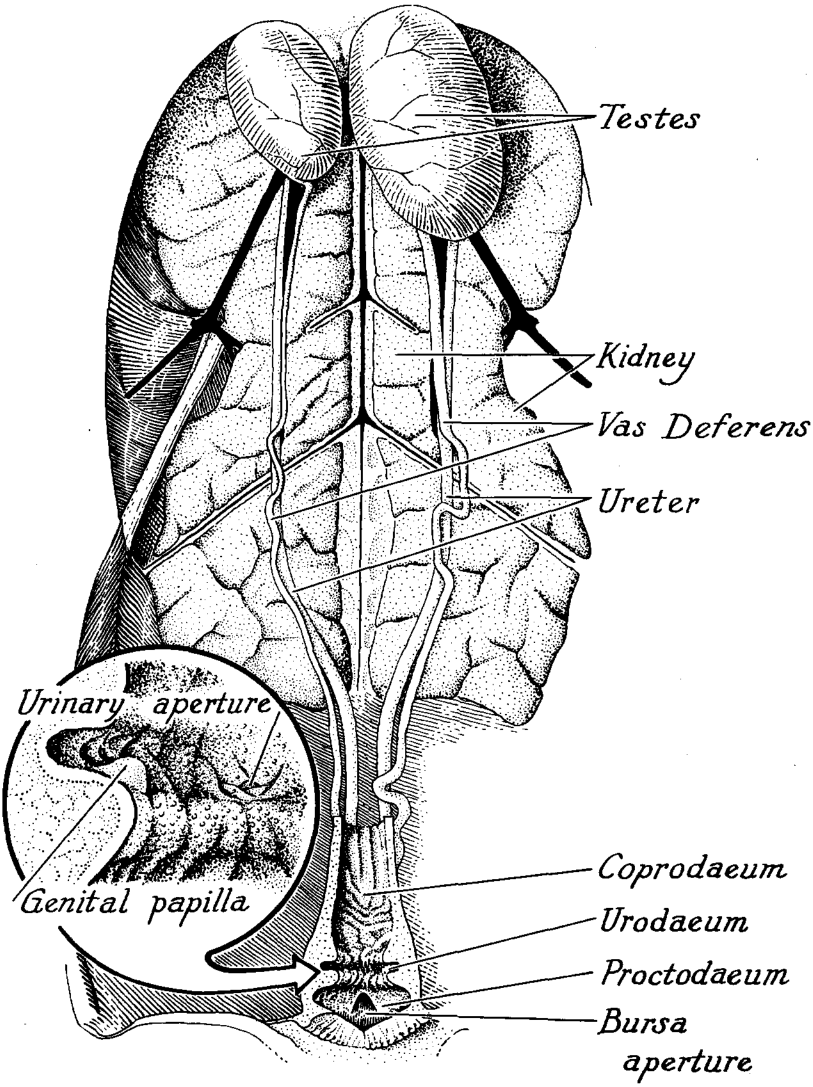

Fig. 1. Male urogenital system of California Quail (*Lophortyx californicus*) in breeding condition.

condition.) The length of each testis was recorded to the nearest tenth of a millimeter after preservation in Bouin's solution. A group of testes was measured before and after preservation and the average shrinkage was found to be two per cent. The larger ones shrank from two to three per cent and the smaller ones shrank from one to two per cent.

Serial sections of 147 testes were prepared as previously described and each testis was assigned to one of six histologic stages.

Histologic Stages

The histologic changes in the testes of California Quail are similar in most respects to those of the Anna Hummingbird (*Calypte anna*) as described by Williamson

(1956:358). Consequently a similar system of stage classification was used. Stages 1 to 5 described beyond are also approximately equivalent to stages 3 to 7 of Blanchard (1941), who studied the reproductive cycle in the White-crowned Sparrow (*Zonotrichia leucophrys*). In addition I have described the sixth stage in the histologic sequence, namely, regression or testicular collapse following the period of sexual activity.

Stage 1 (figs. 2, 3).—The tubules are smallest at this stage. Within each tubule there are from two to four irregular rows of spermatogonia crowding toward the center. Many of these cells are

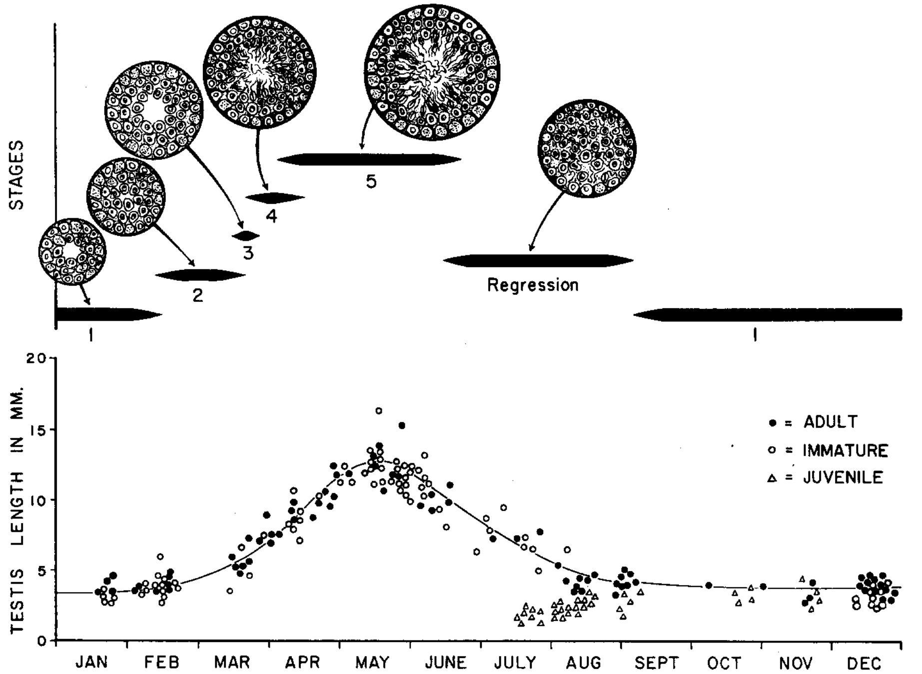

Fig. 2. The growth and regression of the testes in California Quail with associated histology of the seminiferous tubules.

dividing and an occasional primary spermatocyte is seen in the characteristic synaptic condition. The lumen, if present is small. All testes in this stage have pigment granules between the tubules. In some, pigment is very abundant and there is a tendency for it to concentrate on the ventral side of the testis. The tunica albuginea is thin and only slightly fibrous and the nuclei are easily seen. This stage is identical in juvenal, immature, and adult birds with the exception that the tunica in adults is consistently thicker.

Stage 2 (fig. 3).—The tubules are beginning to enlarge and they contain four to seven irregular rows of cells. Those cells on the periphery of each tubule are spermatogonia; in the center, many primary spermatocytes may be seen, most of which are in synapsis. The lumen is consistently absent at this stage and the pigment appears to be less abundant and more evenly distributed than in stage 1. The tunica has become thinner than in the previous stage.

Stage 3 (fig. 3).—The tubules have continued to enlarge and the intertubular spaces are very restricted. From five to ten rows of cells are present within the tubules. Spermatogonia are at the periphery, primary spermatocytes in synapsis in the middle layer, and secondary spermatocytes are next to the lumen which in most tubules is enlarging. Pigment is sparse and evenly distributed. The tunica is the same as in the previous stage.

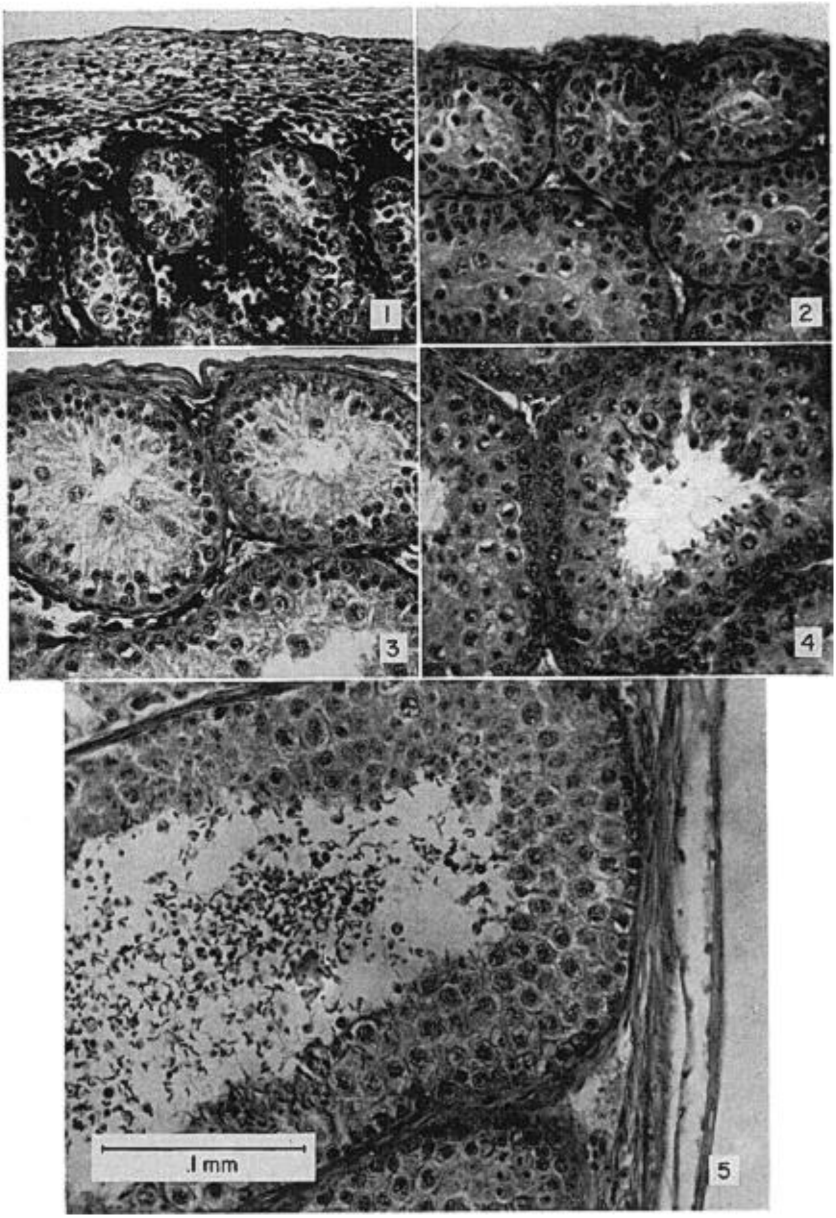

Fig. 3. Histologic changes in the testes of California Quail. Numbers refer to stages as described in text.

Stage 4 (fig. 3).—The tubules are now very large and contain eight to ten rows of cells. Spermatids and maturing sperm in bundles of four to six are seen at the edge of the enlarged lumen with their heads pointing toward the more peripheral layers of cells. An occasional mature sperm may be seen in the lumen. Very little pigment is apparent. The tunica is thinner than in the preceding stage.

Stage 5 (fig. 3).—The tubules have enlarged to their greatest diameter and there are up to ten

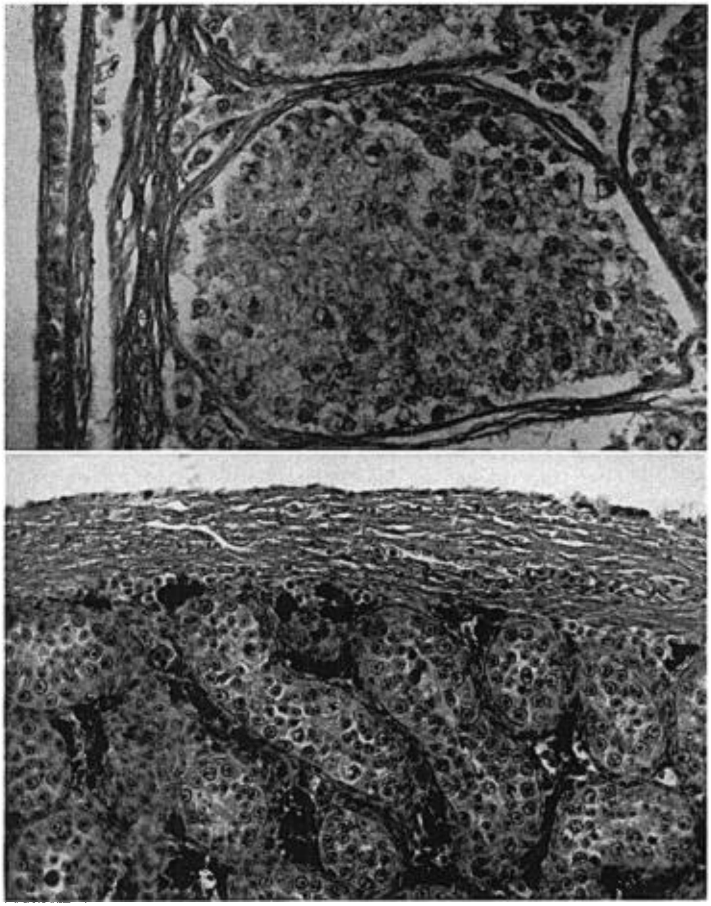

Fig. 4. Early (top) and late testicular regression stages. Magnification is the same as that in figure 3.

rows of cells in each. The lumen has also reached its largest size and contains abundant mature sperm. In addition, the tubules contain cells in all phases of spermatogenesis. The pigment is no longer present in most sections, the tunica is very thin and fibrous, and the nuclei are difficult to see.

Regression (fig. 4).—In the early stage of regression the tubules are collapsed and no lumen is present. The tubules are about equal in size to those in stage 3 and are filled in an irregular manner with cells in all stages of spermatogenesis. There is a medium amount of pigment and comparatively few interstitial cells in the intertubular spaces. The tunica is thicker than in stage 5 and is very fibrous. In most sections it is seen sloughing from the testis.

In the late stage of regression the tubules have almost reached the size of those found in stage 1, and two to three rows of spermatogonia are present. The lumen is present in some tubules, but some degenerating cells are still present in the centers of all tubules. The most conspicuous features of this stage are: (1) the numerous interstitial cells which in some cases surround each tubule in several layers; (2) the abundance of pigment surrounding most tubules; and (3) the thick regenerating tunica albuginea. The nuclei of the tunica are now clearly visible.

Discussion

Figure 2 indicates the annual growth cycle of the left testis of juvenal, immature, and adult birds. The peak of testicular size occurred at the same time (May 18) for each of the three breeding seasons of this study, consequently the data were combined. Included in this figure are diagrammatic representations of the histologic conditions in the seminiferous tubules during the six stages. It is interesting to note the relatively short time span occupied by stages 2, 3, and 4 and the long period of nearly four months that the testis remains in full breeding condition.

The prebreeding testis in both immatures and adults averages 4 mm. in length. The stage 1 condition was found in testes through 4½ mm. in length; stage 2, from 4 to 6 mm.; stage 3, from 6 to 7½ mm.; and stage 4, from 5½ to 9 mm. When a length of 7½ to 8 mm. is reached, mature sperm are found in the lumen of the tubule (stage 5). In general, for every millimeter of growth in testis length prior to breeding, the tissues progress to the next successive histologic stage. The testis continues to grow after stage 5 is reached. While still producing sperm, the testis reaches its average maximum length of 15 mm. and immediately begins to shorten, and it is not until the testis shortens to eight mm. that sperm production ceases. The regressive condition following the collapse of the tubule is found in testes from 10 to 3 mm. in length.

The fact that the growth curves of the testis during the three breeding seasons exhibited the same timing, indicates an independence from immediate environmental conditions such as the temperature and rainfall pattern, as these were shown to be quite different for at least one of the three years. This situation is in contrast to the timing of female gonadal development. The timing of laying seems dependent to some degree on fluctuations in spring weather. The fact that the testis is functional from the first week of April to the last week of June seems an adjustment to the more variable timing of gonadal development in the females. During this study, the males were producing mature sperm three weeks before the date of the earliest egg laid and for a week after the date of the last egg laid.

Spermatogenesis in Immatures

Off season spermatogenic activity has been reported in young of other galliforms. This precocious spermatogenesis occurs in late fall when the days are still long enough to stimulate the gonads. These young of the year are of course not in a refractory condition as are the adults, and in some cases they have been known to produce mature sperm. Kirkpatrick and Andrews (1944), and Hiatt and Fisher (1947) have reported fall testis activity in juvenal Ring-necked Pheasants (*Phasianus colchicus*). Sperm has also been observed in juvenal domestic chickens of 12 weeks of age by Parker, McKenzie, and Kempster (1942). While this phenomenon has not been studied in Bobwhite Quail (*Colinus virginianus*), the potentialities for off-season sperm production have been indicated by Baldini, Roberts, and Kirkpatrick (1952) by stimulating juvenal birds with continuous light to become sexually mature as early as 139 days of age.

The examination of 36 testes of young California Quail from late July through December shows no indication of spermatogenic activity. All testes were in a typical stage 1 condition. In this species it appears that spermatogenesis normally is initiated when young males are about nine months of age and are approaching their first spring breeding season.

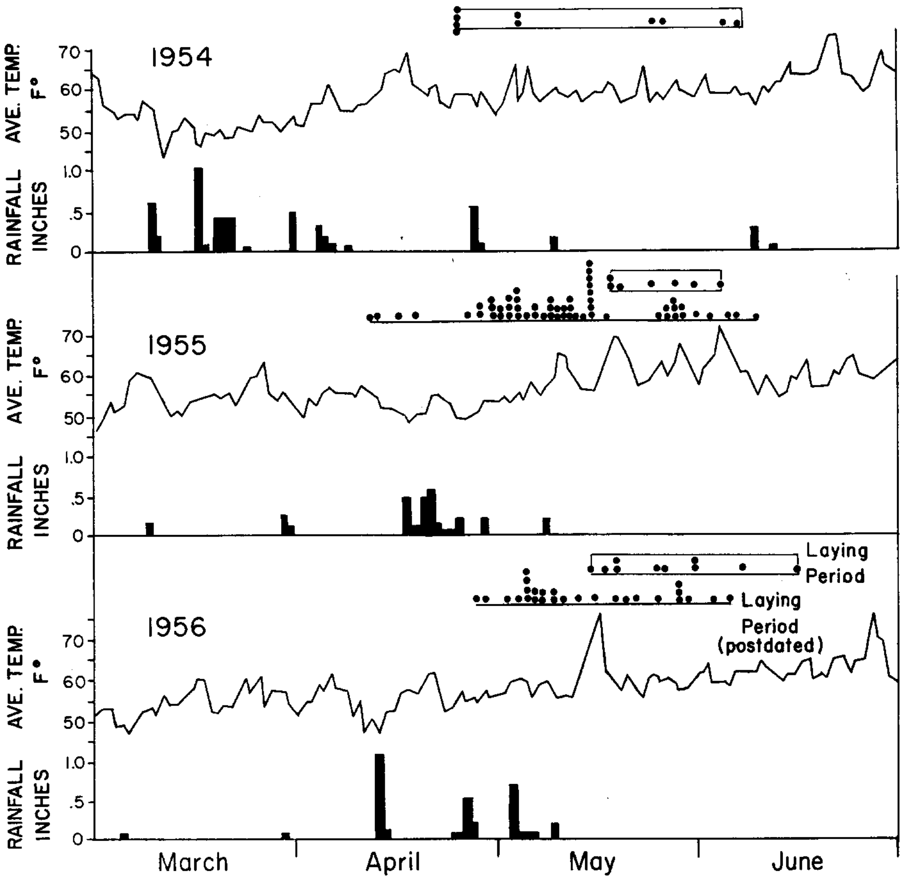

Fig. 5. The laying periods and associated weather conditions on the study area from 1954 to 1956. The horizontal bar depicts the laying periods derived from condition of female reproductive tracts. The dot histograms depict the laying periods postdated by the aging of juveniles during summer and fall.

FEMALE REPRODUCTIVE CYCLE

The present study of reproductive anatomy in the California Quail was extended to include the preovulatory as well as the postovulatory growth of the ovary in both immature birds and adults. The growth and regression of the oviduct in all females was also studied.

The few previous studies of female reproductive anatomy in wild galliforms have been concerned primarily with the condition of the ovary after ovulation. The postovulatory follicles have been studied in pheasants by Meyer, et al. (1947), Kabat, et al. (1948) and by Buss, et al. (1951). The interest in the postovulatory follicle lies in the possibilities of determining the date of laying and the number and condition of the postovulatory follicles. Buss (1946) states that it is possible to count these follicles up to six months after ovulation in Ring-necked Pheasants. It was found in California Quail by gross examination under a dissecting microscope that after 10 days it was impossible to tell a postovulatory follicle from an atretic preovulatory follicle.

Serial sections of an ovary of an adult bird captured in July with an old brood patch, failed to show any clear indications of postovulatory follicles, although atretic unovulated follicles were numerous.

Period of laying.—Figure 5 indicates the laying periods and associated climatological data from 1954 through 1956. The period of laying was determined by examination of the ovaries of laying females. A bird was considered to have started laying if

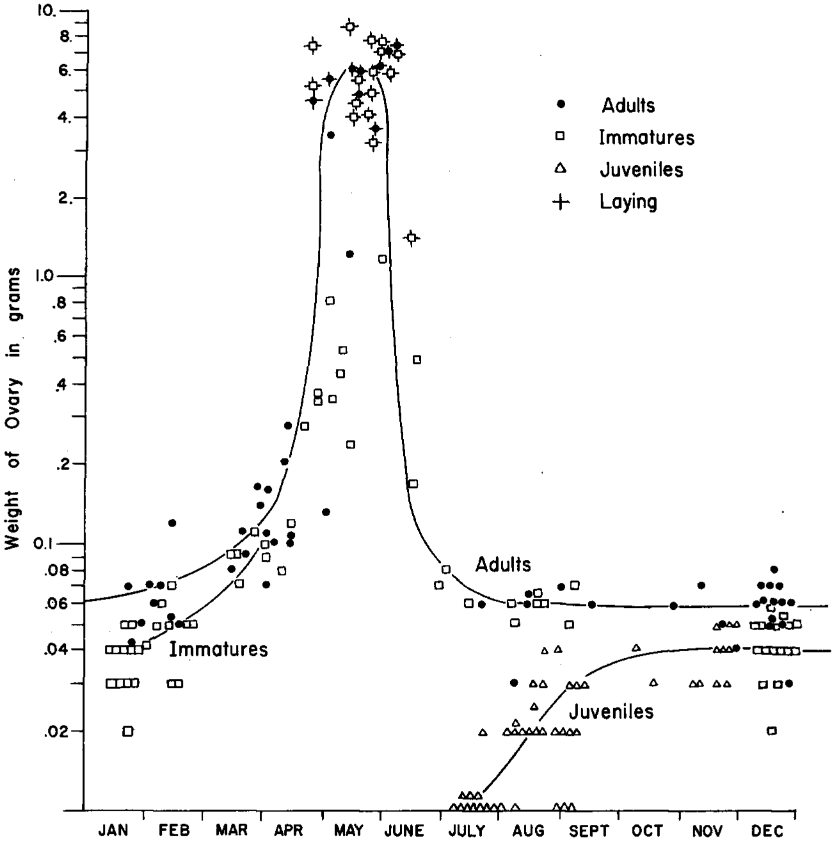

Fig. 6. Annual weight cycle of the ovary in California Quail.

the follicles were large and at least one large postovulatory follicle was present. Laying was considered terminated if the preovulatory follicles were small and numerous postovulatory follicles were present. The duration of laying derived by this means is represented by a horizontal bar for each of the three years.

In addition to the direct method of observing the condition of the reproductive organs of laying females, an indirect method was employed. This consisted of the aging of young birds in summer and early fall by the stage of primary feather replacement and then calculating the date of the first egg in the clutch from which a particular chick was derived. The resulting distribution of laying dates is represented as a histogram in figure 5 for 1955 and 1956.

Considering the laying periods as derived from observation of the ovaries of breeding females, it will be seen that for the three years the laying periods overlap, but

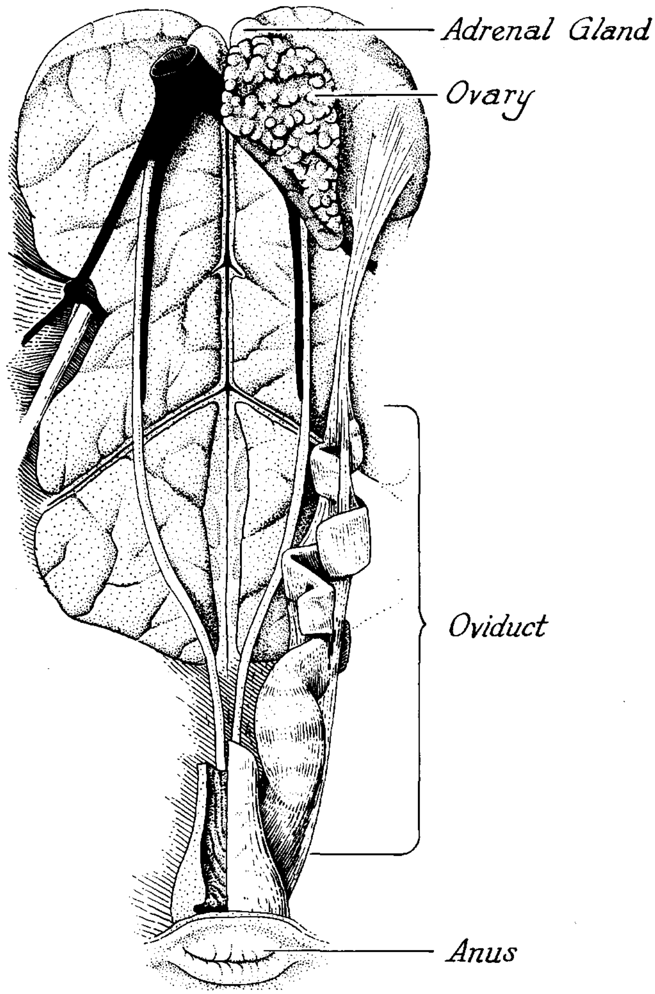

Fig. 7. Typical postbreeding or over-wintering condition of the female reproductive tract in California Quail.

the date of their initiation varies. In 1954, the first eggs were laid on April 24, which is three weeks earlier than the following year when laying started on May 17 and the year after that, when the event was dated on May 14. The distribution of rain and the temperature pattern are similar in 1955 and 1956. In these years when the laying periods began within three days of each other, there was very little rain in March and a great deal in April. In 1954, March had much rain, and April was comparatively dry. The average daily temperature in 1954 may be seen to rise above 55° F. about a month earlier than in the following two years. It is interesting also that the initiation of laying is preceded in 1954 by a period of three weeks during which time the average daily temperature is continually above 55°F. In 1955 and in 1956, respectively, there were periods of only two weeks when average temperatures were above 55°F. In other words, the weather cycle and the laying period during the 1954 season were about

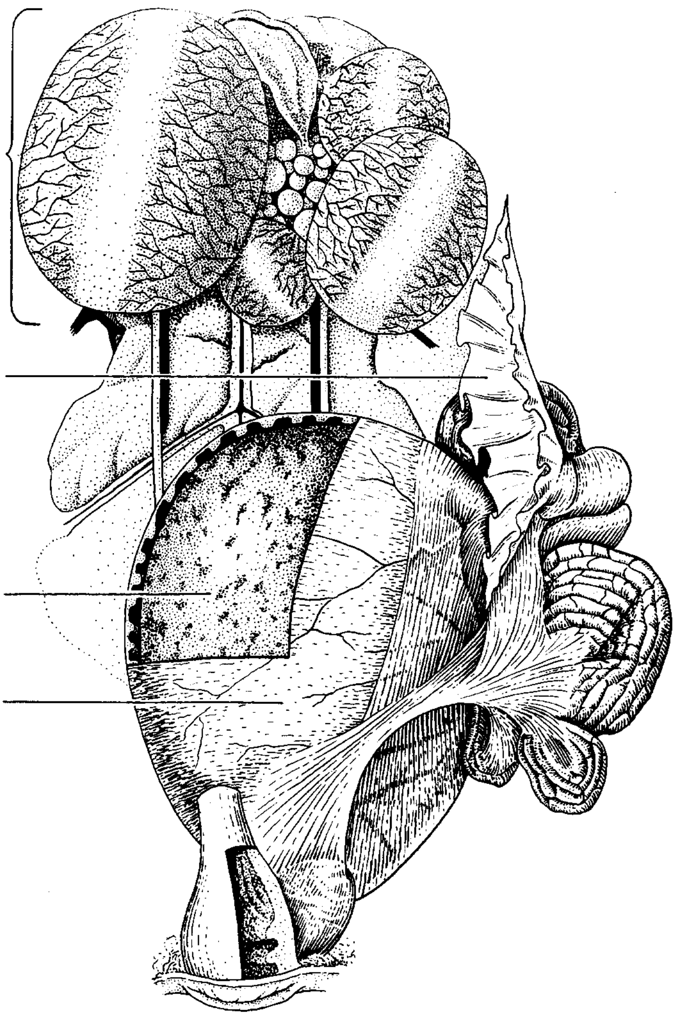

Fig. 8. Reproductive tract of California Quail in laying condition.

a month earlier than the two succeeding seasons. Williams (1959) also reports that in one year of a three-year reproductive study of California Quail in New Zealand the breeding season phenology was delayed three weeks in correlation with unusually heavy precipitation in late spring. A more dramatic correlation of rainfall and female gonadal development is described by Macgregor and Inlay (1951:218) for Gambel Quail (*Lophortyx gambelii*) in the Mohave Desert of California. In this area in 1950, there was only 2 inches of rain which fell in January and, as spring progressed, it was observed that the birds did not form pairs but remained in large winter coveys. Autopsy of quail at this time showed that "male birds possessed slightly enlarged testes, but there was no sign of development of the female reproductive organs." It was not until annuals sprouted in July, following heavy rains, that young quail were observed.

The laying periods during 1955 and 1956, derived indirectly by aging birds of the year utilizing the stage of primary feather replacement, are both considerably earlier

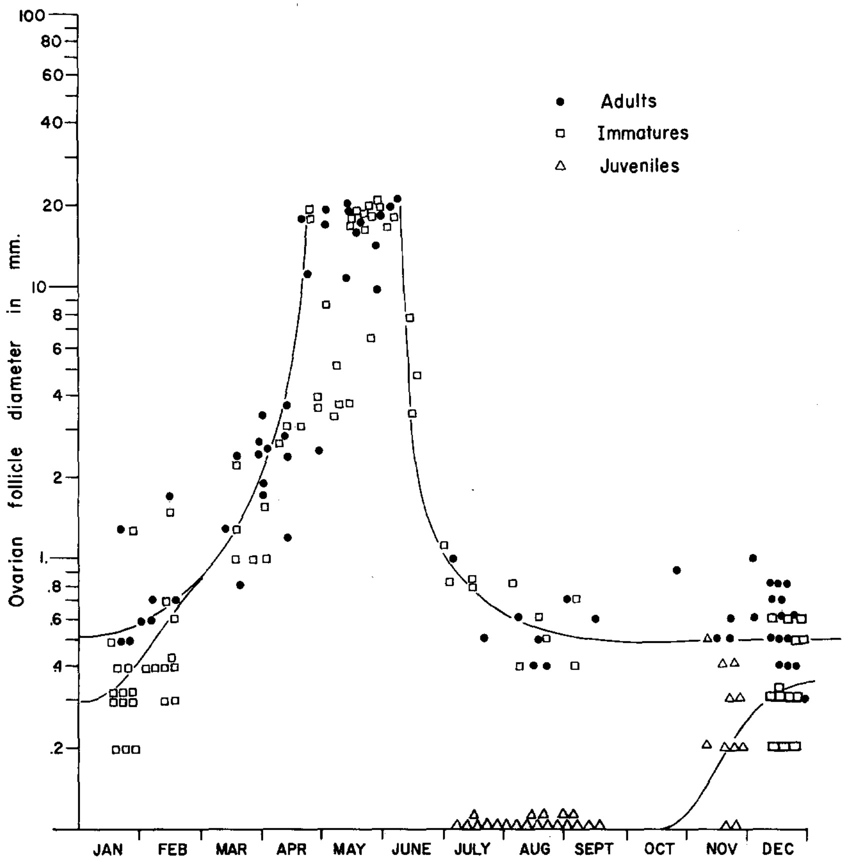

Fig. 9. Annual change in the size of ovarian follicles in California Quail.

and longer than the corresponding period derived by the previous method. This discrepancy may be partly due to errors in the postdating method and perhaps also to an inadequate sample of females early in the breeding season.

Ovary weights.—Ovary weights of the three age classes of quail are presented in figure 6. It can be seen that the ovaries of juvenal females begin to increase in size following hatching and by early November reach the overwintering weight of about 0.04 gm., which is slightly lighter than the winter adult ovarian weight of 0.06 gm. By late January both immature and adult ovaries begin their rapid growth phase. Immature females approach their first breeding season with slightly smaller ovaries than adults, but these soon achieve adult size. Both adults and immature birds begin laying at the same time.

The total weights of ovaries of actively laying birds varied from 3.2 to 8.6 gm. Shortly after the completion of the clutch, and in all cases by July 1, all ovaries were again at their winter weight of approximately 0.06 gm.

Ovarian follicle cycle.—Distinct follicles are not discernible in the ovaries of young females until they are five months old. During the juvenal period, until November, the ovary appears granular and has rows of indistinct protuberances less than a tenth of a millimeter in size. Any one of these small protuberances has the potential of increasing to a structure 200 times its diameter by the following spring. Drawings of the reproductive tract of a nonbreeding female and of a female during the laying period are shown in figures 7 and 8.

The annual variation of the size of ovarian follicles is summarized in figure 9. The greatest width of the largest preovulatory follicle in juveniles, immatures, and adults was recorded to the nearest tenth of a millimeter for the entire sample. It can be seen that even though the ovary is increasing in size, as indicated in figure 8, the follicles remain in a rudimentary condition until mid-November when they begin to enlarge in preparation for the following breeding season. At the end of the year the immature follicles average 0.3 mm. in diameter while those of adults average 0.6 mm. In late January the adult follicles begin to enlarge and by the third week in April both immature and adult birds have ovarian follicles approaching the ovulatory size of 20 mm. Immatures and adults with follicles of ovulatory size are present until the end of the first week of June. No birds with large unovulated follicles were found later than June 10. The unovulated or atretic follicles are rapidly resorbed and by the first week in July the overwintering adult follicle size of 0.6 mm. is reached.

Growth Rate of Preovulatory Follicles and Involution of Postovulatory Follicles

The rate of growth of the prospective ova and the rate of involution of the post-ovulatory follicle, when known, can be used to predict or postdate the time of laying of a particular egg or can be utilized in dating the laying period of a population. In order to construct the growth curve of the follicles and the regression of the post-

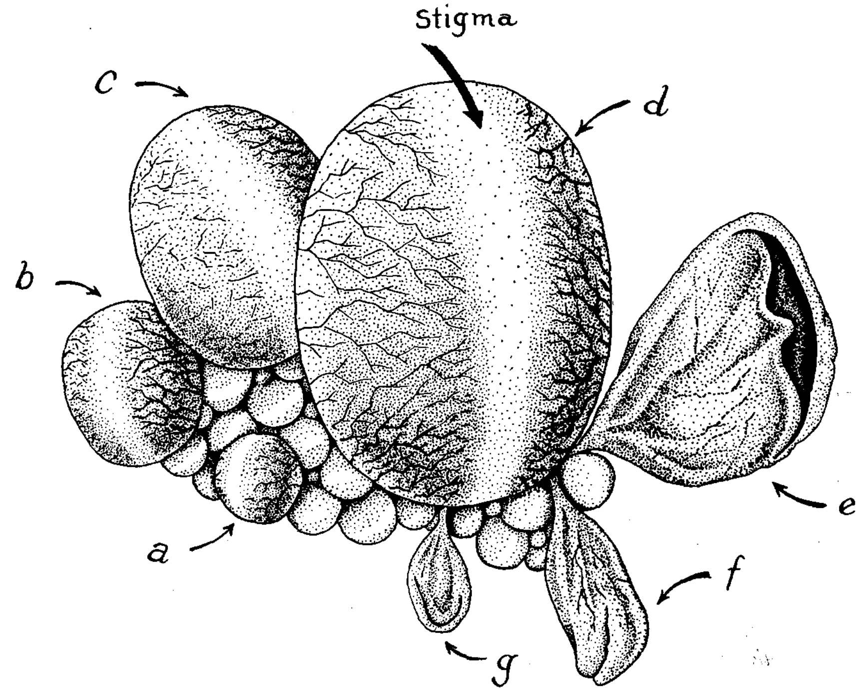

Fig. 10. Ovary of California Quail showing pre- and postovulatory follicles. This ovary is about to ovulate for the fourth time. Letters correspond to those in figure 11.

ovulatory follicles as depicted in figure 11, the date of egg laying must be known. The only reliable laying rate for California Quail comes from Genelly's records (1955:279) of five captive females who averaged, over a month's time, "five eggs per week." This rate of 1.4 days per egg was constant throughout the thirty-day observation period.

The average was taken of the diameters of the preovulatory follicles and the greatest widths of the postovulatory follicles of corresponding age in all of the actively laying females. This measurement was then placed on the graph in a position corresponding to the number of days distant from the day of ovulation. The resulting curve is a smooth one and shows that the initiation of the final growth phase of the prospective ova begins 10 days prior to ovulation. The growth rate is constant from minus seven to minus three days. Beginning three days prior to ovulation the rate declines slightly. This decline in growth rate just prior to ovulation is parallel to that described for domestic chickens by Warren and Conrad (1939).

At ovulation the mature follicle is approximately 20 mm. in diameter. The follicular wall ruptures at the stigma (see fig. 10), which is an avascular area running around the entire follicle, and the ovum is released into the coelom, but it soon passes through the elongate convoluted funnel or infundibular portion of the oviduct. Meanwhile the old covering of the ovum, properly known as the postovulatory follicle, collapses flat and the edges of the ruptured stigma give it the appearance of a flattened tulip. This struc-

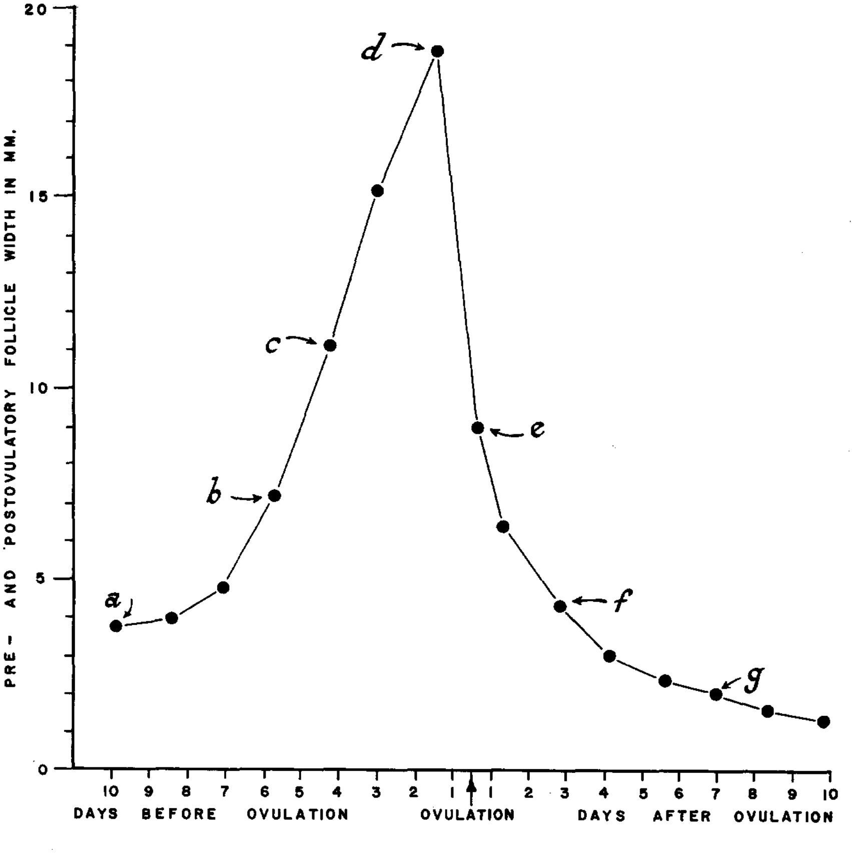

Fig. 11. Growth curve of pre- and postovulatory ovarian follicles. Letters correspond to the morphology shown in figure 10.

ture rapidly involutes from 9 mm. in width directly after ovulation to slightly over one mm. in width 10 days after ovulation. By the tenth day following ovulation the postovulatory follicle has rounded slightly and in most cases the ruptured stigmatic surfaces have healed, rendering it difficult to distinguish from small or atretic preovulatory follicles, even with the aid of a dissecting microscope.

The old postovulatory follicles accumulate an orange pigment while the rest of the ovary remains cream white. It was found that the small size and the irregular outlines of these pigmented structures rendered them extremely difficult to count. By gross observation of a postbreeding ovary one might be certain only that a given female had laid many eggs.

Oviduct cycle.—The oviduct undergoes a dramatic growth phase during the breeding season. It has the capability of increasing its weight 700 fold and is second in its growth potentialities only to the ovary which increases in weight 900 fold during the bird's first year of life. Figures 7 and 8 show the oviduct in nonbreeding and full breeding condition. Note that the infundibular section of this structure does not closely envelop the ovary as is so often indicated in other illustrations of this organ.

Figure 12 shows the annual weight cycle of the oviduct. This organ reaches its

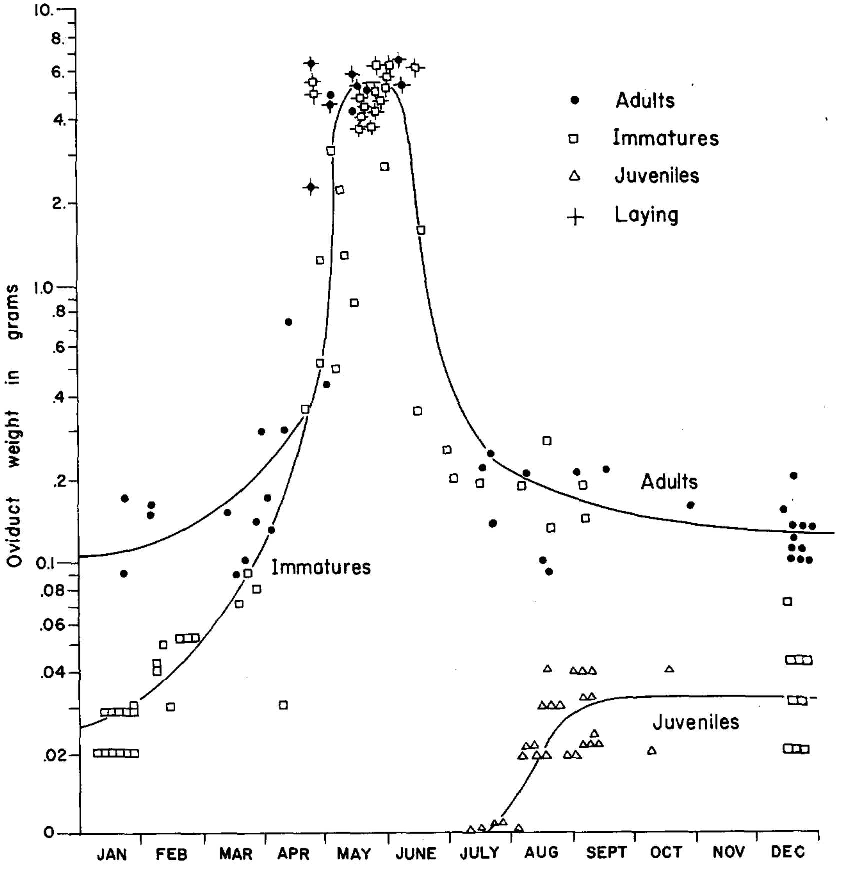

Fig. 12. Annual change in size of oviduct in California Quail. Note that in the fall, birds-of-the-year may be distinguished with certainty from adults by the size of the oviduct.

overwintering weight of 0.03 gm. in juvenal birds by August and remains at this size until the first week in February when it increases in weight rapidly. By the time the first egg is laid in the first week of May, the oviduct averages six grams.

The initiation of rapid growth of adult oviducts prior to laying begins in the first week of April, or two months later than growth of this organ begins in the immature females, but after the first week of April there is no indication of a difference in oviduct growth rate or size between immatures which are approaching their first breeding season and adult birds. The explanation for the time lag in the terminal growth phase of the oviduct in adults lies in the difference in overwintering size of this organ. It may be seen that once an oviduct has fulfilled its reproductive function it never resumes its prebreeding size. Thus its condition may be utilized in separating birds that have never bred from adults that have done so. This criterion can be used with complete confidence through the first eight months of life, or until the first day of March. The critical weight is 0.08 gm. Any female with an oviduct lighter than this has never bred and birds with oviducts heavier than this have bred at least once.

Position of the egg while in the oviduct.—In all the females dissected only 21 had an egg in the oviduct. Three birds had yolk in the magnum portion and 18 had an egg in the uterine portion of the oviduct. All the eggs except two that were in the uterus were situated with their pointed ends caudad. One of these two eggs was crosswise and the other was situated with its blunt end caudad.

It is interesting that even in domestic chickens there still remains doubt as to which end of the egg is presented first at laying. Some workers, Olsen and Byerly (1932), have shown that most eggs appear pointed end first. Bradfield (1951) on the other hand has demonstrated by the use of fluoroscopic examinations of eggs in the posterior part of the oviduct, that for most of the 18 to 20 hours that the egg remains in the posterior portion of the oviduct it lies with the pointed end directed caudally, but just prior to laying it is rotated through 180 degrees and is laid with the blunt end caudad. The data presented here on the position of eggs in oviducts suggests that perhaps California Quail also rotate their eggs just prior to laying and present the blunt end first.

Discussion

In order to discuss the problems of renesting and the possibilities of double broods in California Quail, average values for clutch size, incubation period, and rate of laying must be established. The data on clutch size were taken from three sources. The average number of eggs in which incubation was begun in 16 clutches from the egg collection of the Museum of Vertebrate Zoology was found to be 13.7 eggs. The average of 40 nests reported by Glading (1938) was 10.97 eggs per clutch. An average of 14.20 eggs per clutch has been given by Grinnell, Bryant and Storer (1918). Consequently 14 eggs was considered the average clutch size.

The incubation period is less variable than clutch size. Glading's statement (1938:331) that the incubation period is 22 days was considered accurate. This figure resulted from observations of five successful nests. The average incubation period for Bobwhite Quail is given as 22.5 days by Stoddard (1931:30).

The only reliable data on rate of egg laying for California Quail is from Genelly (1955:279). The methods that were employed to arrive at a laying rate of 1.4 days per egg have been previously discussed.

With the average value of 14 eggs for the clutch size, the rate of laying of 1.4 days for each egg, and the incubation period of 22 days duration, it may be calculated that on the average it takes 19.6 or about 20 days to complete a clutch and a total of 42 days from the laying of the first egg to the hatching of the brood.

If one examines figure 5, keeping in mind that it takes 20 days to complete a clutch, it will be seen that in 1955 the laying period is 19 days long and in 1956 it is 33 days long. It therefore seems that if renesting occurred during these two years, the first nest must have been abandoned very early. Glading (1938) actually observed that most unsuccessful nests were abandoned very early.

The laying period in 1954 was quite different from the two following years in that it was started more than three weeks earlier and extended for a period of 45 days. During a laying period of this length there is ample time for renesting even if clutches were destroyed or abandoned in late stages.

Second broods produced in the same season have been reported occasionally. McLean (1930:19) states that a one-legged female California Quail in one season was observed to have "positively raised two broods to maturity." Second broods in a single season must be extremely rare and the data presented on laying periods for the three years in question in the Berkeley Hills show no indication of double broods.

ANNUAL FLUCTUATION IN BODY WEIGHT

In figure 13, the monthly mean body weights of 374 mature, wild trapped birds are summarized. It may be seen that in general the weights of males and females change in a parallel fashion while the birds are in coveys and in an inverse fashion when they are paired. During the winter months when coveys are intact, the males average seven grams heavier than the females. The continuous weight gain during the late winter months is terminated by March when the males attain their annual maximum of 182.5 gm. The abrupt decline in weight of both sexes from March to April is coincident with covey break up and pairing prior to laying. During May and June the females gain precipitously reaching a level almost 20 gm. greater than the early spring average. In June the females are at their annual maximum of 186.6 gm. and the males are at their annual minimum of 163.1 gm. The females average 23.5 gm. heavier than the males at this time of year. The weight of males during July and August increases and that of the females falls abruptly to the average annual low weight of 157 gm. It is in the period from the latter part of June through August that incubation and rearing of the young birds occurs. There is an indication, despite the small sample, that the males lose weight in October. It is at this time that family groups are assembling to form coveys. During November and December all birds lose weight.

Probable causes of weight fluctuations.—The factors responsible for the nearly 20-gram increment in the females just prior to and during the laying period is obviously due to the increased size of the reproductive organs. The ovary increases from the winter weight of 0.05 gm., to a maximum of 8.6 gm. The oviduct increases from a winter weight of 0.1 gm. (in adults) to a maximum of 6.6 gm., and a shelled egg in the oviduct can weigh as much as 9.5 gm. Figure 13 shows the total weight of female reproductive organs during the breeding season and it may be seen that the area and shape of this curve closely fits that area of the female body weight curve during the breeding period.

A similar pattern of weight gain prior to and during the laying period, followed by weight loss, was also found by Gorsuch (1934) and Gullion and Gullion (1961) in Gambel Quail; by Russell (1931) in Scaled Quail (*Callipepla squamata*); and by Genelly (1955) in California Quail. From October through December both sexes unaccountably lose weight, only to gain it back in January, February, and March.

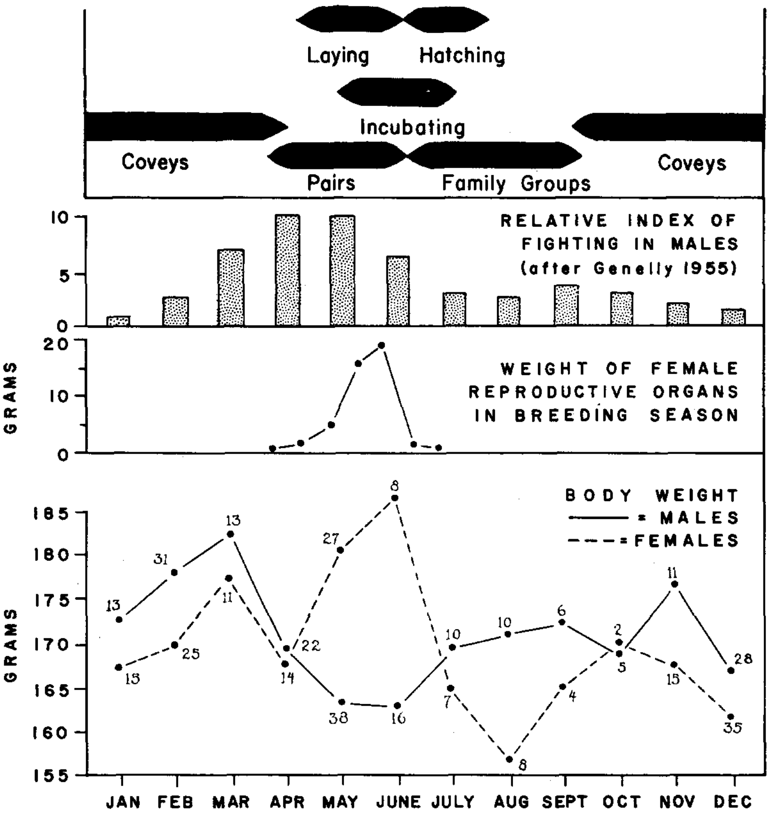

Fig. 13. Annual changes in social structure in California Quail with associated changes in average body weight and aggressive behavior.

The steady decline in the weight of the males from the annual high of 182 gm. in March to the annual low of 163 gm. in June occurs at the time when coveys disperse and when the pair bonds are being established. At this time of the year the males are defending their mates from unmated males and are engaged in other activities accompanying territorial defense. It is thought that weight loss at this time may be due to the stress at the onset of the breeding season accompanied by a reduced intake of food. It may be seen in figure 13 that the incidence of fighting between males is at its maximum prior to and during the breeding season and that there is also another smaller peak of fighting activity in the fall when family groups assemble to form coveys again. This smaller incidence of fighting in fall is also accompanied by weight reduction in males.

During November and December both sexes lose weight and from January through March they gain weight. No positive explanation can be offered for this loss and gain of weight during winter, although it may be pointed out that it is at this time of year that green food is eaten, which is more bulky and perhaps less nutritious than the preferred diet of seeds. It is also known (Lewin, MS) that during winter when the diet is exclusively greens that the intestinal tract increases greatly in length. The small intestine increases to 68 cm. during winter from its summer length of 54 cm.

The caecum increases in winter to a length of 12.5 cm. from its summer length of 8 cm. The length of the intestinal villi also increases in winter as an additional aid in extracting the most nutriment from a low quality, bulky diet. These morphological changes within the digestive tract added to the increased bulk of food may be partly responsible for the increase in body weight at this time. It has also been found by Linsdale and Sumner (1934) that captive birds gain weight during cool temperatures and lose weight during high temperatures. Baldwin and Kendeigh (1938) also state that the body weight of birds is inversely correlated with temperature, being greater in winter and smaller in summer.

GROWTH AND AGING OF YOUNG CALIFORNIA QUAIL

No single method of aging young quail is accurate over the extended period of time from hatching to a little past the first breeding season, but several methods have been devised which may be used with accuracy for various intervals within this time span. No method is known, as yet, that can be used to age quail if they are beyond their first breeding season.

The criteria used to age young quail were devised by recording the growth or regression of various structures which occurred in birds of known age raised in captivity. The eggs were obtained from captives at Davis, California, and were incubated at the Yountville State Game Farm in Napa County. The chicks were then transferred to Berkeley and brooded at 35°C. during the first week and at 24°C. for the next three weeks. They were fed turkey starter mash, lettuce, mixed seeds and water. Of the 103 eggs set, 55 hatched. Of the birds hatched, 33 died in their first week, three died in their second week, and one in the third week. The remaining 18 were successfully raised and were sacrificed periodically to an age of 190 days.

In addition to the chicks of known age, wild ones were taken and aged by the primary feather replacement method of Petrides and Nestler (1943) as described for Bobwhite Quail.

Yolk Sac Resorption

A few days before the embryo hatches, a rapid growth of the tissues at the umbilicus causes that portion of the yolk which has not yet been absorbed to be enclosed within the abdominal cavity. After enclosure of the yolk sac within the body, its utilization goes on as before until it has been entirely used.

The most important external factor influencing the amount of yolk at hatching was found by Romanoff (1944) to be the incubating temperature. He demonstrated in Ring-necked Pheasants and Bobwhite Quail that the greater the deviation from the optimum incubating temperature of 37.5° C., the greater the retention of yolk at hatching. He further states that in Ring-necked Pheasants, Peking Ducks, White Holland Turkeys, and Bobwhite Quail, there is very little effect on the rate of absorption of reserve yolk due to starvation. Similarly Parker (1929) has shown that extreme brooding temperatures did not appreciably change the absorption rate of the yolk nor the future growth rate of the chicks.

In California Quail this residual yolk at hatching is located in a sac situated on the small intestine one-third of the distance from the caecal junction to the gizzard. This material is resorbed rapidly during the first 10 days and then more slowly during the next 20 days. By the end of the first month it is completely gone, leaving no trace of its enclosing membrane on the small intestine. It was found, by measuring the length of this sac, from its insertion into the small intestine to its apex, that the yolk sac length decreased from 9 mm. at hatching to zero by the end of the first 30 days of life. The lengths of the yolk sacs of 22 known-age birds were measured in this manner. These chicks were incubated at a temperature of 38°C. with a relative humidity of 80. The resulting regression curve is presented in figure 14.

The Growth Rate of Young Quail

The published growth curves of young California Quail are not in close agreement. The 15 birds raised in an outdoor pen by Sumner (1935:225) show a slower rate of growth than do the 19 pen-reared chicks raised by Genelly (1955:281). Genelly also shows that the wild birds have a faster growth rate than either of the above pen-reared

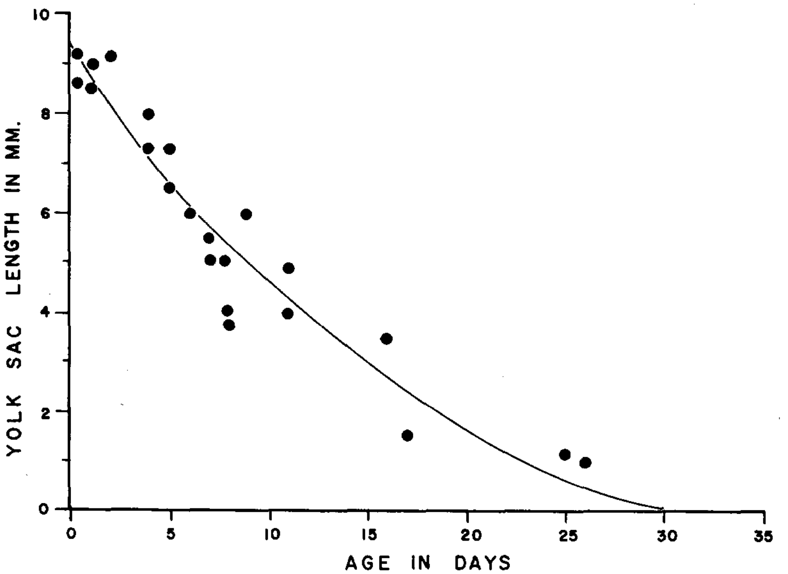

Fig. 14. Resorption curve of residual yolk sac in chicks of California Quail.

groups of young and postulates that a freedom of food choice might account for accelerated growth. Perhaps the lack of parental contact in artificially incubated and brooded chicks precludes not only guidance to desirable food but also prevents the acquisition of a natural intestinal fauna which might assist in the digestion of coarse foods and accelerate growth. On the other hand, the fauna might retard the growth rate.

The intestinal fauna of quail.—In full-grown quail trapped on the study area, the caeca were found to harbor the richest protozoan fauna. Two flagellates, *Trichomonas* sp. and *Eutrichomastix* sp., and a coccidian, *Eimeria* sp., were found. As indicated in table 2, the incidence of the two flagellates is 100 per cent in both males and females. These organisms are present in tremendous concentrations, as determined by using a dilution method and subsequent counting of a known volume in a double ruling haemacytometer. A dilution coupled with a flotation process using a high specific gravity sugar solution after Whitlock (1941) was used to determine the concentration of *Eimeria* oocysts. Both methods give the concentration of organisms per gram of caecal contents. The oocysts of *Eimeria* were found in 78.6 per cent of the males and 84.6 per cent of the females. In none of the over 500 birds autopsied in this study was any pathological condition of any part of the gastrointestinal tract found.

TABLE 2

THE PROTOZOAN FAUNA IN THE CAECUM OF CALIFORNIA QUAIL

	Trichomonas sp.	*Eutrichomastix* sp.	*Eimeria* sp.
MALES			
Number examined	32	32	14
Number positive	32	32	11
Incidence (per cent)	100	100	78.6
Average concentration of organisms/gram	10.1×10^7	12.2×10^8	25.3×10^3
FEMALES			
Number examined	28	28	13
Number positive	28	28	11
Incidence (per cent)	100	100	84.6
Average concentration of organisms/gram	17.9×10^7	11.1×10^8	6.2×10^3

Investigations by Sunde, Cravens, Elvehjem, and Halpin (1950) to discover the sites of vitamin synthesis revealed that the caeca of fowl contained 10 times as much biotin and two times as much riboflavin and niacin as the duodenal loop, the small intestine, or the feces. Couch, et al. (1950) reported also in fowl that folic acid was found to be six to eight times as high in the caeca as in the rest of the tract. Johansson, Sarles, and Shapiro (1948) also found that the site of greatest concentration of microorganisms was found to be in the caeca. Food particles are known to be retained in this organ longer, and thus there is more time for this large population of organisms to digest the material and produce these vitamins. It has also been shown by Suomalainen and Arhimo (1945) that the Capercaillie (*Tetrao urogallus*), Black Grouse (*Lyrurus tetrix*), Hazel Grouse (*Tetrastes bonasia*), and Willow Grouse (*Lagopus lagopus*) possess a caecal fauna capable of digesting the cellulose in coniferous needles. They were able to show that cultures of bacteria from the caeca of older birds were better able to decompose cellulose *in vitro* than were cultures from younger birds.

Effect of intestinal fauna on growth rate.—In order to test the hypothesis that the intestinal fauna has an effect on growth rate, two groups of chicks were reared under the same brooder and fed the same food: turkey starter mash, lettuce, mixed seeds, sand, and water. The control group started with 33 chicks and was kept protozoan free merely by avoiding direct contact with the contaminated chicks and any object that had been associated with them. A partition constructed of a double layer of wire cloth with cardboard in the middle was successful in keeping the two groups of chicks from exchanging intestinal protozoans while being brooded together.

The experimental group started with 21 chicks which were initially contaminated orally at the age of four days with about a cubic millimeter of a fresh caecal dropping from an adult female with a thriving fauna. Fresh caecal droppings were also mixed with the drinking water. This procedure was continued daily until all the birds showed the full complement of protozoans in their caecal droppings. Birds from both groups were weighed daily for the first 70 days, then they were weighed once every few days until the experiment was terminated after 122 days. The mortality was heavy in both groups and at the termination of the experiment four sterile birds and three contaminated ones remained. None of the control birds ever showed protozoans in their droppings and all the birds in the experimental group were successfully contaminated.

Both groups were admittedly small by the termination of the experiment but the pattern of decreasing growth rate in the contaminated group is striking. As may be seen in figure 15, the growth of the contaminated group began to fall short of the control group beginning with the ninth day, or five days after the young quail were initially contaminated. The first contaminated bird showed protozoa in its caecal casts at the age of 24 days, and thereafter the growth rate became markedly less than that in uncontaminated birds. By the 31st day all the innoculated birds showed caecal protozoa. This was also the day when the rate had diverged the greatest from the sterile group. After the 31st day there apparently was an adjustment period and the growth rate was again accelerated and paralleled that of the sterile group. The sterile birds reached their peak size of about 163 gm., or 10 gm. greater than that of the contaminated birds, at 120 days.

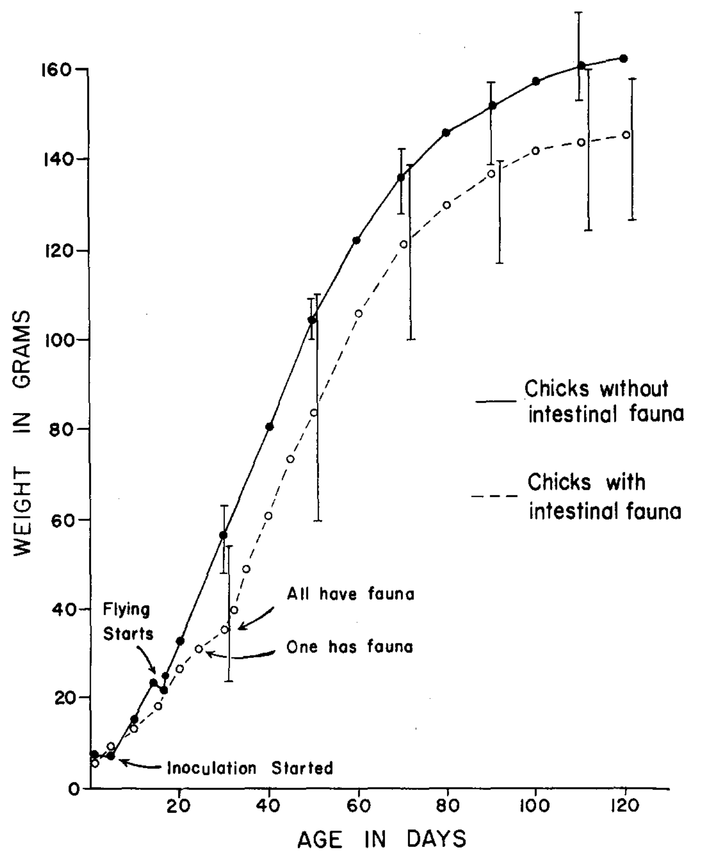

Fig. 15. Growth curve of California Quail with and without normal intestinal fauna.

The association of caecal protozoans with decrease in growth rate seems to indicate that these micro-organisms have a temporary depressing effect on the rate of development from which the birds never fully recover. It is also of interest that Richardson (1939) has shown that caecectomized young chickens gained more weight than controls which harbored flagellates and amoebae in their caeca.

Presumably the presence of an intestinal fauna is advantageous to adult gallinaceous birds in helping them to digest coarse foods high in cellulose. However these organisms quite clearly are something of a burden in the intestinal tracts of chicks, at least as judged by the effect on growth rate.

Growth and Involution of the Bursa of Fabricius

The separation of game birds into age classes in the fall is difficult in those species which have similar immature and adult plumages. In all the galliforms studied thus far the bursa of Fabricius, a lymphatic organ opening into the dorsal side of the proctodial portion of the cloaca (as shown in fig. 16) has proved a reliable structure for separating young of the year from adults. The immature birds in general have a large bursa at least into the first winter of life. The adults have a much smaller or non-measurable bursa. Measurement of the depth of the lumen of the bursa has been used as an aging device by Gower (1939) for Ruffed Grouse (*Bonasa umbellus*), Sharp-tailed Grouse (*Pedioecetes phasianellus*), Prairie Chickens (*Tympanuchus cupido*), Spruce Grouse (*Canachites canadensis*), Hungarian Partridge (*Perdix perdix*), and Woodcock (*Philohela minor*); by Linduska (1943), Leopold (1948), Buss (1946), and Kirkpatrick (1944) for Ring-necked Pheasants; by Hochbaum (1942) and Elder (1946) for waterfowl; by Petrides (1950) for Mourning Doves (*Zenaidura macroura*); and by Riddle and Tange (1928) for Ring Doves (*Streptopelia decaocto*) and domestic pigeons.

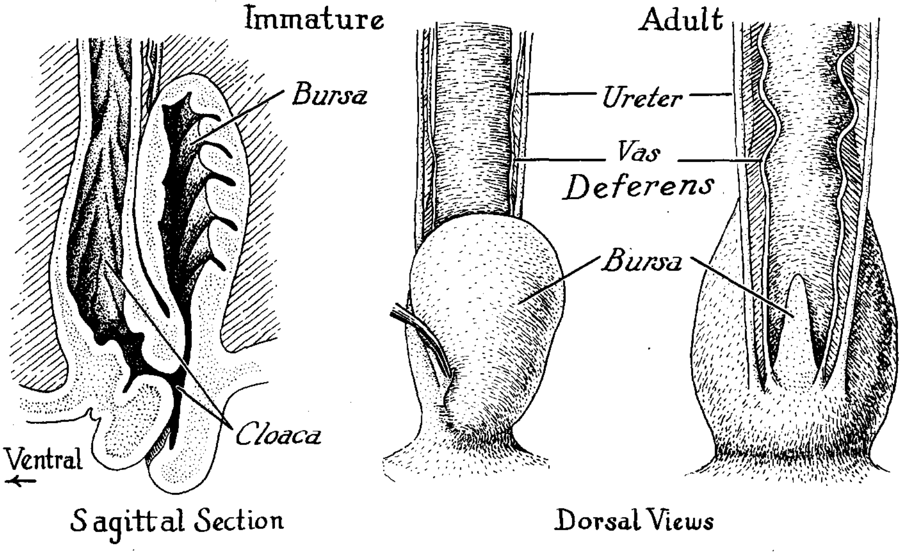

Fig. 16. Sagittal and dorsal views of the bursa of Fabricius in immature and adult California Quail. Probe at left side of center figure indicates where ureter was attached.

The literature on the bursa in relation to game birds is primarily concerned with its size during winter and no account appears of its morphological changes from hatching through the bird's first and second years of life. It is believed that the usefulness of this organ in game birds as an age indicator may be expanded by such a study.

In order to illustrate the morphological changes in the bursa a group of birds of known age reared in captivity and some trapped on the study area and aged by primary feather replacement were utilized. In all cases the greatest external length and width of the bursa along with the weight were taken after preservation in Bouin's solution. The linear measurements were taken with dial calipers to the nearest 0.1 mm. and the weight was recorded to the nearest 0.01 gm. No essential difference was found between the bursal lengths and widths in quail during their first 180 days of life. Within this time the bursa is as wide as it is long. The primary reason for selecting the greatest external bursal width as an indicator of bursal activity was because this measurement alone is 100 per cent reliable in separating birds of the year from adults in a fall and winter sample measured either fresh or after preservation. The external length of the bursa in well grown birds of the year and adults is essentially the same. The typical adult bursa is a long, thin, narrow structure without a lumen. The traditional length taken by cloacal probing is not practicable in preserved specimens.

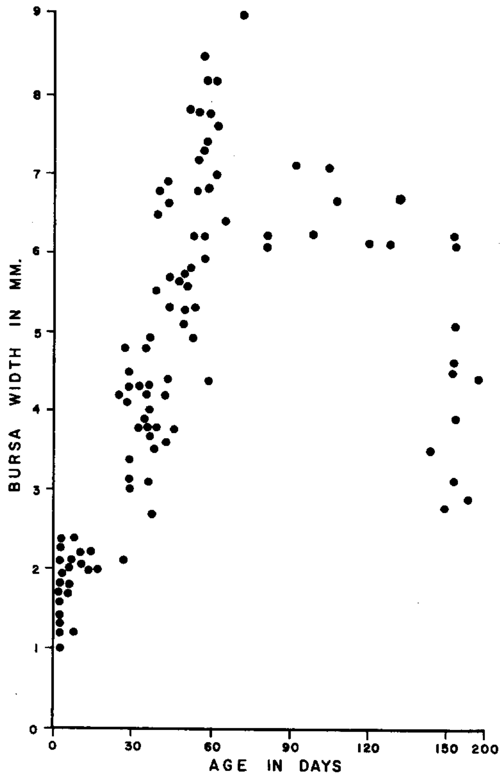

Fig. 17. Growth and regression of the bursa of Fabricius in California Quail of known age.

The greatest external bursal width is easily measured in both preserved and live birds. In the latter this measurement may be taken simply by making a half-inch longitudinal incision between the vent and the tail vertebrae and gently probing to expose the bursa. The live birds that were measured in this manner were not kept long enough to see if this incision would heal without complications, but presumably it would.

Growth and regression of the bursa of Fabricius in birds of known age and in birds aged by primary replacement is shown in figure 17. This figure indicates that at hatching the bursa is two millimeters in width. It is white and bilobed at this time and undergoes rapid growth to reach its maximum size of from 8 to 9 mm. in width (and length) at an age of nine weeks. At this stage it is light cream in color and broadly lobate in shape with a constricted attachment to the proctodaem. Immediately after reaching maximum size it begins to involute and by 150 days it has reached the winter width

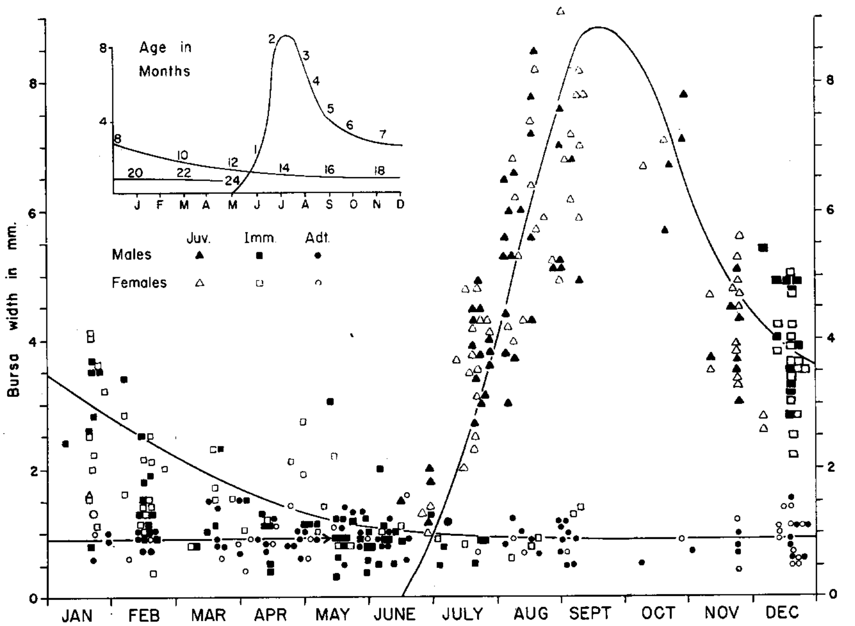

Fig. 18. Variation in size of the bursa in California Quail during the first two years of life.

of between 3 and 4 mm. No differences were found between the bursae of males and females regarding gross morphology or the timing of the growth or involutionary stages of their development.

Figure 18 illustrates the variation in bursal width in juvenal, immature, and adult birds in a typical annual cycle. All measurements were taken from wild trapped quail from the study area from October, 1953, to March, 1957. The data showed no variation from year to year and so were combined.

With regard to the use of the bursa as a criterion of age, it may be seen that through December there is a 100 per cent separation of birds of the year and adults on the basis of bursal widths. Those birds which have a bursal width greater than 2 mm. are birds of the year, and those which have a bursal width less than this are adults. By early June of the following year, that is, at the attainment of one year of age, the bursae are involuted to a width of about 1 mm., which is the adult size.

It is of interest that if one plots external bursal length, there is almost complete overlap between birds of the year and adults in a winter sample. This is due to the large external length of adult bursae. But, of course, if length is taken by probing the lumen of the bursa from the interior of the cloaca, these involuted, closed bursae are recorded as "short" or "absent" and are readily distinguished from those belonging to birds of the year.

The bursa was not found in all of the birds studied. In 52 birds of the 485 dissected, this organ was not demonstrable. Most of these birds were females captured during the breeding season when the enlargement of the oviduct and the increased amount of connective tissue and fat in the cloacal region made the bursa very difficult to find. Following the breeding season the bursa is again detectable.

It is believed that the bursa persists in nearly all, of not all California Quail regardless of age, and that in cases where no bursa can be demonstrated, the explanation lies in the inability of the investigator to find it.

Aging Juveniles by Primary Feather Replacement

In young quail, the juvenal primaries are replaced in an orderly manner starting with primary number one and proceeding distally through primary number eight. The new primaries are retained through the first winter and first breeding season, following which all ten primaries are replaced in the first annual molt. The buff-tipped juvenal upper primary coverts are retained over the first winter and serve to distinguish immatures from adults until shortly after the first breeding season.

A method of aging young birds was described by Petrides and Nestler (1943) who constructed curves from the growing primaries of Bobwhite Quail. These growth curves of the first winter primaries of the Bobwhite have subsequently been compared to those of California Quail by Genelly (1955) and Raitt (1961), who found no essential difference in these birds approaching their first winter in regard to time and rate of primary feather replacement.

SUMMARY

This study was concerned with the annual reproductive events during a three and one-half year period in a population of California Quail (*Lophortyx californicus brunnescens*) living in Strawberry Canyon near Berkeley, California. In addition to trapping wild quail from the study area, young birds were hatched and reared in captivity in order to establish accurate means of aging young quail and to determine what effect the normal complement of intestinal protozoans had on the rate of growth.

Seasonal changes in the male reproductive tract are described grossly and histologically. The timing of testicular recrudescence during the three breeding seasons was almost identical despite the fact that the pattern of spring weather was quite different during one of the three years. Males were capable of inseminating females, as evidenced by free spermatozoa in the seminiferous tubules, during a ten-week period in the spring.

The laying periods averaged four weeks in duration and occurred well within the potential inseminating period of the males, but not on identical dates each year. Spring weather seemed to modify the sexual cycle in females, whereas it did not affect the cycle in males.

Aging techniques employing the well-known methods based on primary feather replacement and condition of greater upper primary coverts were used. In addition, a comprehensive study of growth and involution of the bursa of Fabricius and the yolk sac are described.

By a process of postdating from an aged sample of quail taken in late summer, it was possible to determine the average hatching date, the average date of initiation of incubation, and the average date of the onset of laying.

A means was also developed to age preovulatory and postovulatory follicles within ten days of the time of laying. This then is a second and more direct method of establishing the date of the onset of laying.

A thriving intestinal fauna which is a normal inhabitant of birds in this population is described. Tremendous numbers of micro-organisms are found in the caeca and are presumably beneficial to adults but they were shown to have a retarding effect on the rate of growth of young quail.

Data were obtained on the annual variation in body weight of adult quail. In the females, the spring weight gain followed by a summer loss is due to growth of the ovarian follicles and the oviduct. The weight loss in males is associated with fighting that occurs during pairing and covey formation.

LITERATURE CITED

Baldini, J. T., Roberts, R. E., and Kirkpatrick, C. M.
1952. Studies of the reproductive cycle of the bobwhite quail. Jour. Wildl. Manag., 16:91–93.

Baldwin, S. P., and Kendeigh, S. C.
1938. Variations in the weight of birds. Auk, 55:416–467.

Blanchard, B. D.
1941. The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool., 46:1–177.

Bradfield, J. R. G.
1951. Radiographic studies on the formation of the hen's egg shell. Jour. Exp. Biol., 28:125–140.

Buss, I. O.
1946. Wisconsin pheasant populations. Wisc. Cons. Dept., Madison, Wisconsin., Publ. 326, A-46:1–184.

Buss, I. O., Meyer, R. K., and Kabat, C.
1951. Wisconsin pheasant reproduction studies based on ovulated follicle technique. Jour. Wildl. Manag., 15:32–46.

Couch, J. R., German, H. L., Knight, D. R., Sparks, P., and Pearson, P. B.
1950. Importance of the cecum in intestinal synthesis in the mature domestic fowl. Poultry Sci., 29:52–58.

Elder, W. H.
1946. Age and sex criteria and weights of Canada geese. Jour. Wildl. Manag., 10:93–111.

Genelly, R. E.
1955. Annual cycle in a population of California quail. Condor, 57:263–285.

Glading, B.
1938. Studies on the nesting cycle of the California valley quail in 1937. Calif. Fish and Game, 24:318–340.

Gorsuch, D. M.
1934. Life history of the Gambel quail in Arizona. Univ. Ariz. Biol. Sci. Bull. No. 2:1–89.

Gower, W. C.
1939. The use of the bursa of Fabricius as an indication of age in game birds. Trans. Fourth N. Amer. Wildl. Conf., 426–430.

Grinnell, J., Bryant, H. C., and Storer, T. I.
1918. The game birds of California (Univ. Calif. Press, Berkeley).

Gullion, G. W., and Gullion, A. M.
1961. Weight variations of captive Gambel quail in the breeding season. Condor, 63:95–97.

Hiatt, R. W., and Fisher, H. I.
1947. The reproductive cycle of ring-necked pheasants in Montana. Auk, 64:528–548.

Hochbaum, H. A.
1942. Sex and age determination of waterfowl by cloacal examination. Trans. Seventh N. Amer. Wildl. Conf., 299–307.

Johansson, K. R., Sarles, W. B., and Shapiro, S. K.
1948. The intestinal microflora of hens as influenced by various carbohydrates in a biotin-deficient ration. Jour. Bact. 56:619–634.

Kabat, C., Buss, I. O., and Meyer, R. K.
1948. The use of ovulated follicles in determining eggs laid by the ring-necked pheasant. Jour. Wildl. Manag., 12:399–416.

Kirkpatrick, C. M.
1944. Body weights and organ measurements in relation to age and season in ring-necked pheasants. Anat. Rec., 89:175–194.

Kirkpatrick, C. M., and Andrews, F. N.
1944. Development of the testis in the ring-necked pheasant. Anat. Rec. 89:317–324.

Leopold, A. S.
1948. The pheasant kill on the Conway Ranch—1947 and 1948. Mus. Vert. Zool., Univ. Calif., Berkeley, 14 pp. mimeo.

Linduska, J. P.
1943. A gross study of the bursa of Fabricius and cock spurs as age indicators in the ring-necked pheasant. Auk, 60:426–437.

Linsdale, J. M., and Sumner, E. L., Sr.
1934. Variability in weight in the golden-crowned sparrow. Univ. Calif. Publ. Zool., 40:309–320.

Macgregor, W., Jr., and Inlay, M.
1951. Observations on failure of Gambel quail to breed. Calif. Fish and Game, 37:218–219.

McLean, D. D.
1930. The quail of California. Calif. Fish and Game, Game Bull. No. 2:1–47.

Mayr, E.
1939. The sex ratio in wild birds. Amer. Naturalist, 73:156–179.

Meyer, R. K., Kabat, C., and Buss, I. O.
1947. Early involutionary changes in the post-ovulatory follicles of the ring-necked pheasant. Jour. Wildl. Manag., 11:43–49.

Olsen, M. W., and Byerly, T. C.
1932. Orientation of the hen's egg in the uterus and during laying. Poultry Sci., 11:266–271.

Parker, J. E., McKenzie, F. F., and Kempster, H. L.
1942. Development of the testes and combs of white leghorn and New Hampshire cockerels. Poultry Sci., 21:35–44.

Parker, S. L.
1929. Effects of early handicaps on chickens as measured by yolk absorption and body weight to twenty weeks of age. Hilgardia, 4:1–56.

Petrides, G. A.
1950. Notes on determination of sex and age in the woodcock and mourning dove. Auk, 67:357–360.

Petrides, G. A., and Nestler, R. B.
1943. Age determination in juvenal bob-white quail. Amer. Midl. Nat., 30:774–782.

Raitt, R. J., Jr.
1961. Plumage development and molts of California quail. Condor, 63:294–303.

Richardson, F. L.
1939. Cecectomy of chicks and its effect upon their growth and infectability with intestinal flagellates. Amer. Jour. Hyg., 30:69–71.

Riddle, O., and Tange, M.
1928. Studies on the physiology of reproduction in birds. XXIV. On the extirpation of the bursa Fabricii in young doves. Amer. Jour. Physiol., 86:266–273.

Romanoff, A. L.
1944. Avian spare yolk and its assimilation. Auk, 61:235–241.

Russell, P.
1931. New Mexico's scaled quail investigation. Trans. Eighteenth Amer. Game Conf., 226–273.

Stoddard, H. L.
1931. The bobwhite quail: its habits, preservation, and increase (Charles Scribner's Sons, New York).

Sumner, E. L., Jr.
1935. A life history study of the California quail, with recommendations for its conservation and management. Calif. Fish and Game, 21:167–342.

Sunde, M. L., Cravens, W. W., Elvehjem, C. A., and Halpin, J. G.
1950. The effect of diet and cecectomy on the intestinal synthesis of biotin in mature fowl. Poultry Sci., 29:10–14.

Suomalainen, H., and Arhimo, E.
1945. On the microbial decomposition of cellulose by wild gallinaceous birds (family Tetraonidae). Ornis Fennica, 22:21–23.
Warren, D. C., and Conrad, R. M.
1939. Growth of the hen's ovum. Jour. Agric. Res., 58:875–893.
Whitlock, J. H.
1941. A practical dilution-egg-count-procedure. Jour. Amer. Vet. Med. Assoc., 98:466–469.
Williams, G. R.
1957. Changes in sex ratio occurring with age in young California quail in Central Otago, New Zealand. Bird-Banding, 28:145–150.
1959. Aging, growth-rate and breeding season phenology of wild populations of California quail in New Zealand. Bird-Banding, 30:203–216.
Williamson, F. S. L.
1956. The molt and testis cycles of the Anna hummingbird. Condor, 58:342–366.

Museum of Vertebrate Zoology, Berkeley, California, July 7, 1962. (Present address, *Department of Zoology, University of Alberta, Edmonton, Alberta, Canada.*)