ECOLOGY AND REPRODUCTION OF CALIFORNIA QUAIL IN SOUTHEASTERN WASHINGTON

ROBERT ANTHONY[1]

Department of Zoology
Washington State University
Pullman, Washington 99163

The California Quail (*Lophortyx californicus*) is not part of the native fauna of the state of Washington. According to the records of the Washington Department of Game, the first introduction of 108 birds was made in Walla Walla County in 1914. By 1920, 80 per cent of Adams, Spokane, and Whitman Counties were being cultivated for wheat farming, and at present over 97 per cent is cultivated (Buss and Dziedzic 1955). The California Quail presently attains relatively dense populations in canyons where shrubby vegetation still persists. Today, it is one of the important game birds of this region.

Much is known about the biology of California Quail, but most studies have been conducted near the southerly limits of its range in California. Consequently, this study was designed to obtain information on the ecology and reproduction of this species in Washington. Some phases of the study provide information comparable to the work of Genelly (1955), Lewin (1963), McMillan (1964), and Williams (1967).

THE STUDY AREA

All field work was conducted in southeastern Washington, mostly along the Snake River from 5 mi. S of Asotin to Central Ferry, but also including Asotin Creek, Union Flat Creek, the Palouse River, and Steptoe, Wawawai, and Almota Canyons (fig. 1). The topography of the area is characterized by undulating loessal soils over basalt, which outcrops frequently along the slopes of valleys.

HABITAT COMPLEXES

Based on physiognomy and present agricultural practices in southeast Washington, there are four "habitat complexes" which quail inhabit and which differ in microclimate and plant species. They include (1) a Snake River Lowlands Complex, including the lower river terrace and the present flood plain; (2) a Snake River tributaries Complex, including Asotin Creek and Steptoe, Wawawai, and Almota Canyons; (3) a Wheatland Complex; and (4) a Palouse River-Ponderosa Pine Complex. The following discussion of the four habitat complexes is modified from material suggested by Dr. Rexford Daubenmire (pers. comm.).

The Snake River Lowlands are occupied primarily by cattle and fruit ranches, and overgrazing is almost universal along the river and rocky canyon slopes. The dominant tree species are hackberry (*Celtis douglasii*) and willow (*Salix* spp.). Willow occurs predominantly at the river's edge, whereas *Celtis douglasii* extends up the slopes of canyons a short distance. Sage brush (*Artemisia rigida*), smooth sumac (*Rhus glabra*), and rabbit brush (*Chrysothamnus nauseosus*) are the dominant shrubby species. Of the grasses, cheatgrass (*Bromis tectorum*), drop-seed (*Sporobolus cryptandrus*), and wheatgrass (*Agropyron spicatum*) are the most important.

The Snake River tributaries are characterized by permanent streams bordered with brush. Little or no cultivation is possible in these areas. The dominant tree species are white alder (*Alnus rhombifolia*), chokecherry (*Prunus virginiana*), *Philadelphis lewisii*, and hawthorn (*Crataegus douglasii*), which occurs higher on the canyon slopes. Snowberry (*Symphoricarpos albus*) and rose (*Rosa* spp.) are the dominant shrub species on the north-facing canyon slopes, whereas *Artemisia rigida* and *Rhus glabra* grow on the drier south-facing slopes. *Agropyron spicatum* and bluegrass (*Poa secunda*) are the most abundant grasses. Blackberry (*Rubus laciniatus*), locally introduced, is a valuable species in the ecology of California Quail.

The Wheatland Habitat Complex comprises the majority of the study area, since more than 97 per cent of Whitman County is under cultivation. Wheat (*Triticum aestivum*) and peas (*Pisum sativum*) are the prominent plants of this complex. The native vegetation, where it has not been greatly disturbed, exhibits plants characteristic of the rolling hills of loessal deposits. The dominant tree species is *Crataegus douglasii*. *Symphoricarpus albus* and *Rosa* spp. are important shrub species, and *Festuca idahoensis* is the dominant grass.

The Palouse River-Ponderosa Pine Complex, as its name implies, is characterized by *Pinus ponderosa*. The presence of this species indicates a wetter microclimate than the other three complexes. The lower bottoms of the Palouse River are dominated by thickets of *Crataegus douglasii*, *Symphoricarpos albus*, and *Rosa* spp. On the drier south-facing slopes of the Palouse River Canyon, grasses become more important with *Agropyron spicatum* and *Poa secunda* being dominant. The north-facing slopes are mainly pine-covered.

METHODS

Collections by shooting began in February 1967 and continued until October; additional specimens were acquired from hunters between then and January 1968. Observations of behavior were recorded prior to collections during the breeding season.

[1] Present address: Arizona Cooperative Wildlife Research Unit, University of Arizona, Tucson, Arizona 85721.

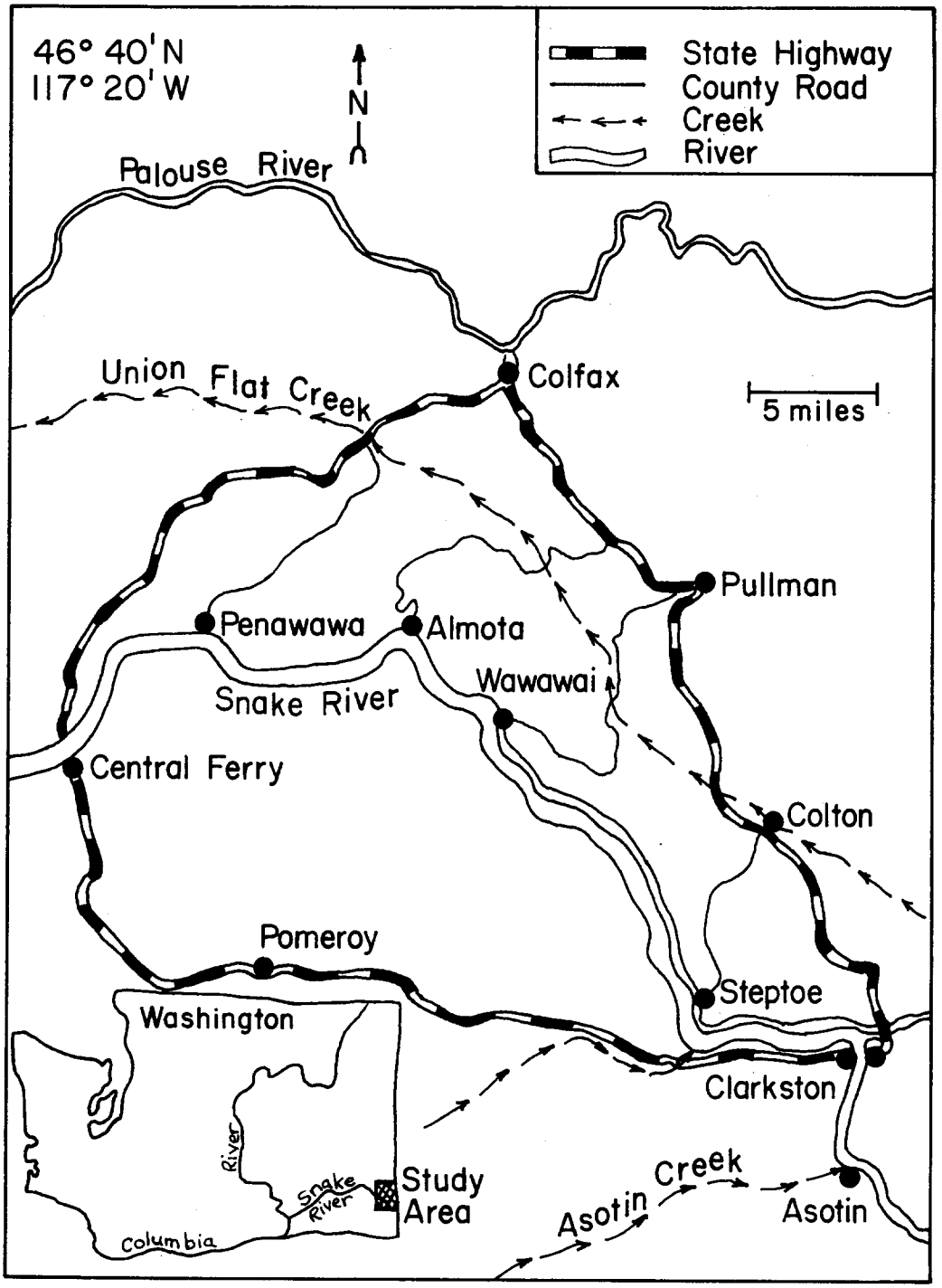

FIGURE 1. Study area of California Quail in southeastern Washington.

FIELD PROCEDURES

Reproductive organs were removed immediately after collection and placed in AFA solution. They were allowed to remain in this fixative for approximately 24 hr, at which time they were transferred to a 10 per cent formalin solution for storage. Total body weights were recorded to the nearest 0.1 g, and the left wing of each specimen was saved for molt analysis and a permanent record of age. Crops were removed, weighed, and saved for further analysis. Weekly counts of birds were made in the field, and sex ratios were recorded when possible. Brood studies were conducted throughout May, June, July, and August 1967. Location, date, and age of young were used to eliminate multiple observations on the same brood. From many broods one member was collected to acquire an estimation of age, utilizing development of the primaries (Raitt 1961).

TABLE 1. Sex and age ratio[a] of California Quail from southeastern Washington for 1967.

Sex-age group	Spring Mar.–May		Summer June–Aug.		Fall Sept.–Nov.		Winter Dec.–Feb.	
	n	%	*n*	%	*n*	%	*n*	%
Adult males	150*	22.9	130*	8.0	62*	18.8	40	22.3
Adult females	82*	12.5	69*	4.2	36*	10.9	25	14.0
Immature males	203	31.0	274**	16.9	—	—	63	35.2
Immature females	220	33.6	207**	12.8	—	—	51	28.5
Juvenile males	—	—	483	29.8	117	35.5	—	—
Juvenile females	—	—	459	28.3	115	34.8	—	—
Total	655	100	1622	100	330	100	179	100

[a] Totals and overall sex ratios for each season were acquired from field observations. Age ratios within each sex were obtained from collections during spring and summer, and from hunters during fall and winter. These age ratios were used to calculate (estimate) the number of birds in each age group within each sex. Percentages follow from the estimated number of birds in each sex-age category for each season.
* Difference between sexes statistically significant, $P < 0.05$; ** $P < 0.003$.

LABORATORY PROCEDURES

Reproductive organs were weighed (from formalin) to the nearest 0.001 g and measured to the nearest 0.1 mm. Weight and diameter of the first through the fifth largest nonovulated follicles were recorded after dissection from the ovary.

Microslides were prepared routinely of the left testis. Tissues were dehydrated through the standard alcohol-benzene series and embedded in Waterman's paraffin. Sections were taken from approximately the middle of each testis, cut at 8 μ, and stained with Heidenhain's hematoxylin.

METHOD OF SAMPLING AND STATISTICAL DESIGN

The technique employed by Krumrey and Buss (1969) was used to analyze testes slides; a reticle with a 200-square grid was inserted into the drawtube of a microscope. The reference points used in the cell counts were the 200 intersection points of the squares. To eliminate bias, fields within slides were selected by the use of a table of random numbers obtained from Fisher and Yates (1949:104–109). Sample size was determined by Stein's formula (see Steel and Torrie 1960).

The statistical analysis of testicular tissue consisted of an analysis of variance of a hierarchial model (Steel and Torrie 1960) with unequal numbers of observations. The model is mixed with the stages (S) of spermatogenic activity fixed, age group (A) fixed, birds (b) within stage-age classifications random, and grids (e), or samples within birds, random. The model is:

$$Y_{ijkl} = u + S_i + A_{ij} + b_{ijk} + e_{ijkl}.$$

The model states that the amount of testicular tissue counted (Y_{ijkl}) in the k^{th} bird ($k = 1,2,\ldots,75$) of the j^{th} age group ($j = 1,2$) in the i^{th} stage ($i = 1,2,\ldots,5$) is a linear function of the grand mean u, the fixed stage effect (S_i), the fixed age effect (A_{ij}), and the random bird effect (b_{ijk}). The errors (e_{ijkl}) are assumed to be normally and independently distributed with mean zero and homogeneous variance.

SEX AND AGE RATIOS

The basic terminology used here for denoting age is after Williams (1957) and Lewin (1963). "Juvenile" refers to any young bird that had not completed the postjuvenal molt; "immature" is any bird that had completed the postjuvenal molt but not the first postnuptial molt; and "adult" refers to a bird that had completed the first postnuptial molt. According to Raitt (1961), completion of the postjuvenal molt occurs around the twenty-first week of life. Buffy upper primary converts and pointed primaries 9 and 10 distinguish immatures from adults.

The number and percentage of quail in the different sex and age classes are presented in table 1. The overall sex ratio favored males, there being 120 males to 100 females (54.6 per cent males). Males typically outnumber females in populations of California Quail (Emlen 1940; Storer et al. 1942; Williams 1957, 1963; Lewin 1963; McMillan 1964; Raitt and Genelly 1964). Assuming a 1:1 sex ratio at fertilization and no differential mortality between sexes throughout life, there should be unity of sex ratios for all age groups during all periods of the year. (Unity can be thought of as acceptance of the null hypothesis of no difference in the number of males and females at the 0.05 level of significance.) The juvenile sex ratios show unity; χ_1^2 (chi-square value with one degree of freedom, computed from figures in table 1) equals 0.611 ($P = 0.450$) and 0.017 ($P = 0.897$) for summer and fall, respectively. There was no significant difference between the number of immature males and females for winter and spring: $\chi_1^2 = 1.263$ ($P = 0.267$) and 0.685 ($P = 0.426$), respectively. The summer sex ratio of immatures, however, was significantly different, ($\chi_1^2 = 9.332$, $P = 0.003$), indicating a differential mortality of females during their first breeding season. Emlen (1940) and Williams (1963) have also reported a high mortality among immature females going through their

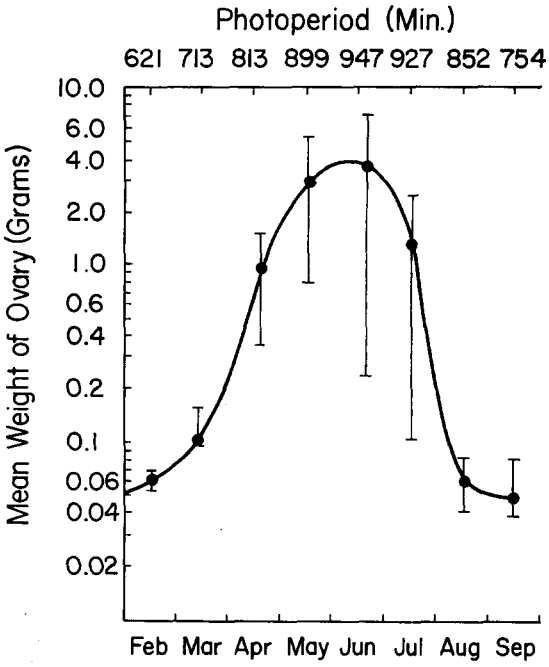

FIGURE 2. Mean monthly ovary weights with associated photoperiod in California Quail of southeast Washington. (Vertical bars indicate 95 per cent confidence intervals.)

first breeding season. Sex and age ratios show that adult females were definitely the minor sex-age group. There was a significant difference ($\chi_1^2 = 3.841$, $P = 0.05$) between the number of adult males and females for the spring, summer, and fall seasons. The lack of a significant difference for adults during the winter ($\chi_1^2 = 3.461$, $P = 0.067$) is probably a reflection of small sample size. Williams (1963) believes that the breeding female among California Quail populations suffers greater risks and stresses during laying and incubation of eggs and the caring of young than does the male. Kabat et al. (1956) found that resistance to stress (starvation) among hen Ring-necked Pheasants (*Phasianus colchicus*) was least following egg laying and that this ability to withstand applied stress was directly related to the bird's weight. Apparently, females suffered high mortality during the breeding season in the present study.

FEMALE REPRODUCTIVE CYCLE

The sequence and pattern of changes in weight, size, and macroscopic appearance of the ovary, ovarian follicles, and oviduct were analyzed from a sample of 62 specimens collected 9 February–7 October 1967. Cyclic changes in the female reproductive organs are discussed according to the four natural stages of the annual cycle: wintering condition or quiescence, recrudescence, breeding, and regression. The number of ovulated follicles was not used to determine first egg dates because it is difficult to distinguish a 10-day postovulatory follicle from an early-stage preovulatory follicle in California Quail (Lewin 1963).

OVARIAN CYCLE

Mean monthly ovary weights for the breeding season of 1967 are presented in figure 2. Recrudescence of the ovary began around the middle of February and continued through March, April, and early May. The gradual increase in weight and size during early recrudescence was accelerated shortly before the start of egg laying. Considerable variation in ovary weights occurred during late recrudescence as seen by rather wide confidence intervals. This variability is caused by variation in the time of laying the first egg by individual females. Both adult and immatures began laying at approximately the same time, so this is not a cause of variability. The entire period of recrudescence involved a period of about 10–12 weeks.

The mean monthly size of the ovaries reached a peak during the early part of June; this is in close correlation with the longest daily photoperiod (fig. 2). Ovary weights were highest and females were laying for approximately two months from May to early July. Renesting attempts came in July. Lewin (1963) indicates that breeding activity was highest during May for female California Quail near Berkeley, California, in 1954–1956, which is approximately a month earlier than the laying peak of California Quail for the present study. This difference in the peak of the breeding season is in accordance with Baker (1938), who related breeding phenology in birds to latitude. In the present study the wide variation in ovary weights during June and July was apparently caused by the regression of the ovary after incubation for some females, while others were still laying or renesting. According to Mackie and Buechner (1963), the time of ovulation in relation to the time of collection will also cause some variation.

Ovaries regressed during late June, July, and August as incubation was completed. Soon after incubation, regression of the ovary was exceedingly rapid and further regression through August was slow. Most ovaries had reached their wintering condition by September. The entire period of regression was approximately eight weeks, much shorter than the period of recrudescence.

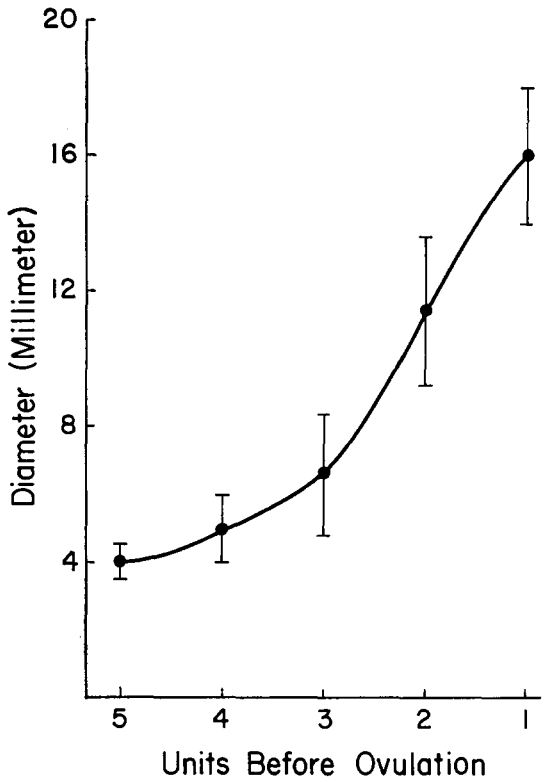

FIGURE 3. Mean diameters of successive maturing preovulatory follicles in California Quail. (Vertical bars indicate 95 per cent confidence intervals.)

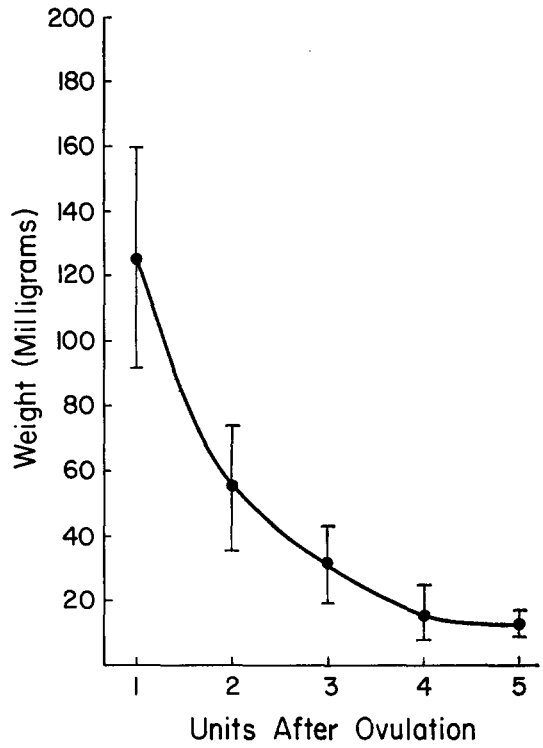

FIGURE 4. Mean weights of successive regressing postovulatory follicles in California Quail. (Vertical bars indicate 95 per cent confidence intervals.)

OVARIAN FOLLICLES

Mean diameters of successive maturing follicles from the ovaries of laying females are presented in figure 3. "Units" on the horizontal scale represent follicles before ovulation; one unit is equivalent to 1.4 days per egg laid, the laying rate of California Quail (Genelly 1955). Growth of the ovarian follicles from seven to four days before ovulation was slow. Thereafter follicles developed rapidly with an average daily increment of 3 mm. Three days prior to ovulation, growth decreased slightly, a decline parallel to that described for domestic chickens by Warren and Conrad (1939) and for California Quail by Lewin (1963). The largest ovarian follicle was usually 14–18 mm, but at the time of ovulation it was about 20 mm. The rate of involution of postovulatory follicles for California Quail was similar to that of the Ring-necked Pheasant (Meyer et al. 1947) and the Chukar Partridge, *Alectoris graeca* (Mackie and Buechner 1963). Postovulatory follicles involuted rapidly during the first three days after ovulation (fig. 4). Involution during later days was slower. After seven follicles have been ovulated, (approximately 10 days), they are difficult to identify macroscopically.

OVIDUCT CYCLE

Mean monthly oviduct weights for the 1967 breeding season are presented in figure 5. Recrudescence of the oviduct began in late February, and weight increase was slow through the first two weeks of March. In the later phase of recrudescence, there was a very rapid development and growth of the oviduct. The period of oviduct recrudescence was approximately 8–10 weeks, compared with 10–12 weeks for ovarian recrudescence. Thus, recrudescence of the oviduct was more rapid and reached completion earlier than recrudesence of the ovary.

Oviducts were at maximum size during late May and early June, corresponding to the peak of hatching in mid-June (fig. 10). Oviduct weights were highest for about three months between late April and early July. Evidently, the oviduct maintains its functional status longer than the ovary. Regression of the oviduct began in July and was practically complete by mid-August. Regression of the oviduct, like the ovary, was rapid for three to five days post-incubation but conspicuously slower

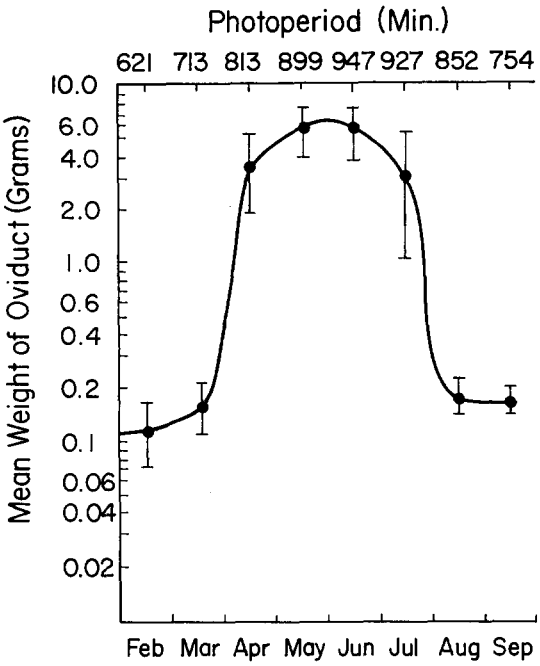

FIGURE 5. Mean monthly oviduct weights with associated photoperiod in California Quail of southeast Washington. (Vertical bars indicate 95 per cent confidence intervals.)

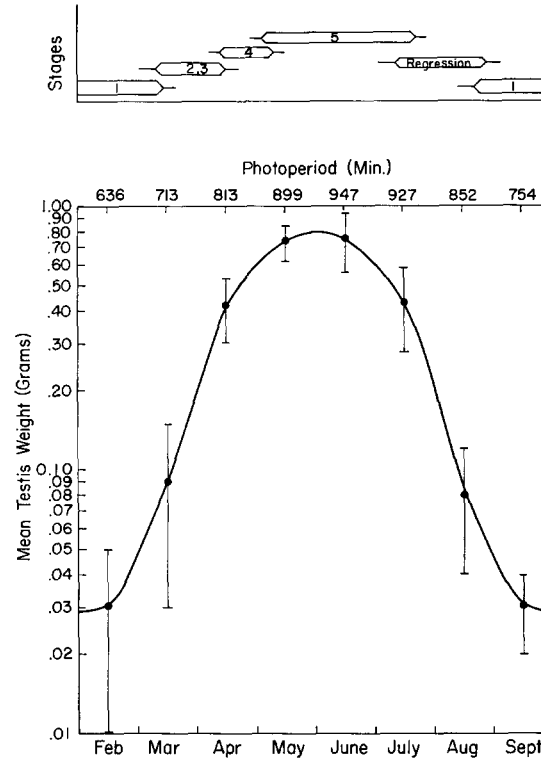

FIGURE 6. Mean monthly testes weights with associated stages of spermatogenesis and photoperiod in California Quail of southeast Washington. (Vertical bars indicate 95 per cent confidence intervals.)

thereafter. Oviducts reached their wintering condition by late September, but did not regress to an immature condition as did the ovaries. Oviducts showed less variation in weight during the breeding season than did the ovaries. The postnuptial molt of females did not begin until shortly after eggs hatched, and regression of the reproductive organs was usually not complete. Thus, recrudescence of the ovary and oviduct could occur if nest destruction occurred during incubation. Seubert (1952) found that renesting of Ring-necked Pheasants can occur within a few days after a nest has been destroyed during any stage of incubation.

MALE REPRODUCTIVE CYCLE

Three criteria were used in determining the stages in the reproductive cycle of male California Quail in the present study: (1) weight and length changes of the testes, (2) spermatogenic activity as determined by histological analysis, and (3) behavioral changes during the breeding season. This part of the study is based on 75 male specimens (48 immatures and 27 adults) collected February–September 1967. An analysis of testicular histology was used for two reasons: (1) to compare the breeding potential of adult and immature males and (2) to compare the rate of testicular regression of males rearing a brood with those not rearing one. The histological sequence of recrudescence and regression of the testes for California Quail described by Lewin (1963) is similar to that of the present study and will not be discussed. However, Lewin's stages 2 and 3 of spermatogenic activity were combined in the present study for statistical reasons. Since stage 3 is very short in duration, very few specimens collected were in this stage. Combining stages 2 and 3 created a sample of sufficient size to warrant statistical tests, and the variance of stage 2 and 3 combined did not differ significantly ($P > 0.05$) from variances of other stages. As a result, 5 stages of spermatogenic activity are discussed here: (1) wintering condition, (2 and 3) early recrudescence, (4) late recrudescence, (5) breeding condition, and (R) regression.

TESTICULAR CYCLE

The growth cycle of the testes and the associated photoperiod and seasonal distribution of histological stages of spermatogenesis are given in figure 6. Recrudescence of the testes began around mid-February and continued through April. The entire period of recrudes-

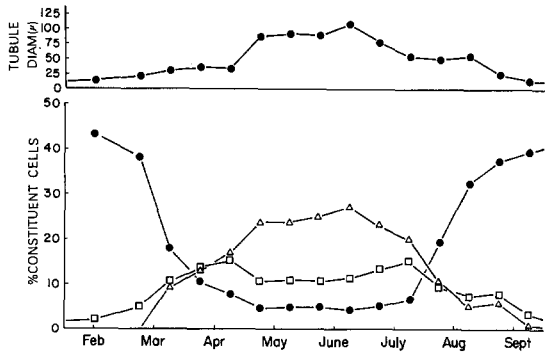

FIGURE 7. Developmental history of seminiferous epithelium and tubule lumen in California Quail of southeast Washington. Filled circles represent spermatogonia; open squares, spermatocytes; open triangles, sperm-spermatids.

cence involved about 10 weeks. Increase in testis weight was rapid from the start of recrudescence but declined in late April and May. Wide confidence intervals for February reflect a small sample size, since variation was small. In March, however, there was much variation in testis weight, associated with the variation in time when recrudescence began for individual males.

Testicular weights reached a peak during late May and the first part of June. Lewin (1963) indicates that testes of California Quail were in breeding condition during April, May, and June in California for 1954 and 1955. Testes in the present study were in breeding condition during May, June, and July. Thus, gonads of both sexes indicate that the breeding season of California Quail in Washington lags a month behind that of quail in California.

Highest testes weights did not correlate directly with breeding condition of the testes as determined histologically. Quail were able to maintain testes in breeding condition, histologically, while both testicular weight and photoperiod were decreasing (see stage 5 of fig. 6). Males in the present study were, therefore, in breeding condition longer than females.

Testes began to regress in late June and continued regressing through July and August. Regression of testes, like recrudescence, was very rapid, and most had reached the wintering condition by late August.

The developmental history of the seminiferous epithelium and tubule lumen before, during, and after the breeding season is presented in figure 7. The percentage of spermatogonia in the tubules of birds in the wintering condition was high and those of other seminiferous elements low. A decided break in the curves occurs at about mid-March as recrudescence began. At full breeding condition sperm and spermatids were the most abundant cell types, spermatocytes were intermediate in abundance, and spermatogonia least abundant. The actual number of spermatogonia did not seem to change, but their relative abundance did. Near the end of July there is another decided break in the curves following the beginning of testicular regression. By September, testes were in the wintering condition, and percentages were similar to those in February. The tubule-lumen curve follows the same pattern of changes as the curve for spermatids and spermatozoa.

The testes of California Quail show a pigment variation throughout the breeding season. During fall and winter, they were blue-black, but with the onset of recrudescence they became lighter, and at the height of breeding condition they were pearl white. With regression during late summer, testes became dark again until the next spring. This change is correlated with the abundance of melanin pigment per unit area in the intertubular areas of the testes. According to Serventy and Marshall (1956), this change is the result of pigment dispersal with increase in testicular volume during recrudescence.

STATISTICAL ANALYSIS OF TESTICULAR HISTOLOGY

A statistical analysis was conducted to test the hypothesis that there was no difference in the mean testicular histology of adult and immature California Quail. Slides of the left testes from 75 quail were analyzed and assigned to one of the five stages of spermatogenic activity. The analysis of variance was applied to data for each of three different cell types (spermatogonia, spermatocytes, and spermatid-sperm).

As expected, means for stages of spermatogenic activity are significantly different for spermatogonia, spermatocytes, and spermatid-sperm; with 4 and 65 *df*, the *F*-ratios (and *P* values) for each cell type, respectively, are 93.81 ($P < 0.001$), 2.77 ($P < 0.05$), and 78.47 ($P < 0.001$). The *F*-ratios for the age effect (grand means, table 2) show that there was no significant difference between means of the two age groups for spermatogonia, spermatocytes, or spermatid-sperm ($F = 0.04$, 0.10, and 0.42, respectively, with 1 and 65 *df*). Since the interaction of stage × age was significant for spermatogonia and spermatocytes ($F = 3.21$, $P < 0.025$; $F = 4.45$; $P < 0.005$, respectively, with 4 and 65 *df*), the means for each stage-age combination for each cell type should

TABLE 2. Means and sample size for stage × age interaction in testicular histology of California Quail.

Testis: stage of spermatogenesis[a]	No. spermatogonia				No. spermatocytes				No. spermatid-sperm			
	Adults		Immatures		Adults		Immatures		Adults		Immatures	
	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n
1. Wintering condition	69.93	40*	80.32	110*	14.95	40*	5.90	110*	9.30	40	0.81	110
2, 3. Early recrudescence	42.44	50*	23.67	70*	19.36	50*	27.47	70*	17.36	50	22.56	70
4. Late recrudescence	14.34	50	15.78	50	30.48	50	26.46	70	32.14	50	38.62	50
5. Breeding condition	9.54	110	10.87	190	22.70	110	26.23	190	50.25	110	48.02	190
R. Early regression	13.75	20	25.57	60	25.45	20	22.53	60	34.35	20	25.35	60
Grand mean	25.78	270	31.25	180	22.58	270	21.31	480	33.56	270	29.67	480

[a] Stages of spermatogenesis (from Lewin 1963) may be briefly described as follows: 1 = seminiferous tubule and lumen small, spermatogonia abundant, melanin pigment present, tunica albuginea thick; 2 & 3 = tubule enlarged, but lumen small, primary spermatocytes in cynapsis, pigment sparse; 4 = tubule large, spermatids and sperm present, pigment sparse, tunica thin; 5 = tubule and lumen largest, sperm abundant, pigment absent, tunica thinnest; R = tubule large, but lumen collapsed, cells degenerate, some pigment.

* Difference between adult and immature groups statistically significant at the 0.05 level of confidence.

be compared. These means are presented in table 2. There are no significant differences (at the 0.05 level) between means for the two age groups at stages 4, 5, and R, so the testicular histology of adult California Quail during the height of the breeding season is not significantly different from that of immatures. If there is no difference in the testicular histology of the two age groups, then they are obviously not different in reproductive potential. Considering the population dynamics and particularly the high mortality of California Quail, these findings seem very reasonable. Males going through their first breeding season are equally as capable breeders as are second or third year breeders, as suggested by their monogamous mating and annual recruitment to the population. However, experiences of adult males that have gone through a breeding season probably give them an advantage over immature males in some instances. This would be especially true when competition for the same female is involved.

The reproductive organs of female gallinaceous birds undergo rapid regression after a clutch of eggs has hatched and rearing of the brood begins. Of all broods observed in the present study, 24 per cent were being reared by males only and 69 per cent by both parents. Therefore, the question arose as to whether the stimulus of rearing a brood of young initiated faster regression of the spermatogenic activity in these males than in those not rearing a brood. A second statistical analysis was proposed to test the hypothesis that there was no difference between the mean testicular histology of males rearing a brood and that of those not rearing one. The statistical design used is identical to the previous one except that the fixed age effect (A) is replaced by the fixed brood effect (B). The mean stage effect was again statistically significant for spermatogonia, spermatocytes, and spermatid-sperm (with 2 and 15 *df*, $F = 21.30$, 9.97, and 37.66; $P < 0.001$, 0.005, and 0.001, respectively). The brood effect was not statistically significant for spermatogonia, spermatocytes, or spermatid-sperm (with 2 and 15 *df*, $F = 4.43$, 1.88, and 3.16, respectively). Since the interaction of stage × brood was also not significant ($F = 0.05$, 0.66, and 0.54, with 2 and 15 *df*) the null hypothesis is accepted. Thus, the rearing of a brood initiated no pronounced regression in spermatogenic activity.

BODY WEIGHT FLUCTUATIONS

Male gallinaceous birds of North America are, on the average and with few exceptions, heavier than females during the fall and winter. However, mean weight reverses during the breeding season, with females becoming heavier than males. This change in body weight during the breeding season has been reported for Ring-necked Pheasants (Kirkpatrick 1944; Nagra and Buss 1959), Bobwhite Quail, *Colinus virginianus* (Hamilton 1957), Gambel's Quail, *Lophortyx gambelii* (Gullion and Gullion 1961; Raitt and Ohmart 1966), and California Quail (Storer et al. 1942; Williams 1952; Genelly 1955; and Lewin 1963). Males showed a sharp decline in mean body weight during early spring in the present study, whereas mean female weights increased (fig. 8). Male weights were lowest during July, after which time weights increased. Female weights dropped to a mean low in early August, when most females had incubated. These low body weights for females in early August are correlated with the season of high differential mortality among females, mentioned previously in connection with sex and age ratios.

Presumably, crop weights can be used as an indication of food consumption, since "feeding proceeds intermittently throughout the day

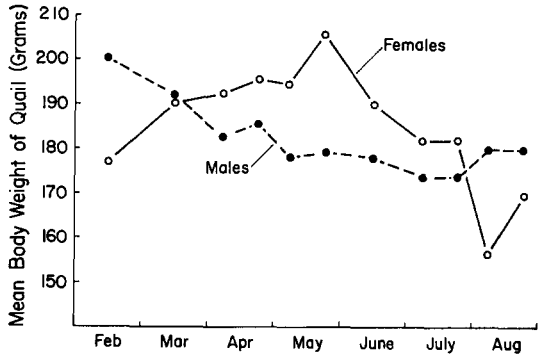

FIGURE 8. Body weight changes of California Quail through the breeding season of 1967.

with stomachs receiving only slow streams of food from the crop" (Sumner 1935:185). The average amount of food consumed by males and females throughout the breeding season, as reflected in crop weights at the time of collection, corresponds to body weight changes of the sexes (figs. 8, 9). Like mean weights, food consumption of the sexes was reversed, compared with the prebreeding season. This, however, is only part of the total picture, since some decrease in body weight for males may be correlated with stressful behavioral changes associated with display, pairing, and aggressiveness during the breeding season. Nagra and Buss (1959) reported that seasonal body weight of female Ring-necked Pheasants paralleled the pattern of growth and regression of the ovary. Also, organs associated with digestion and assimilation of food hypertrophied with increased caloric intake. Increased food consumption in female California Quail seems to be indirectly associated with increase in the size of the reproductive organs.

BROOD STUDIES

The study by Raitt (1961) provides an adequate means for estimating the age of young

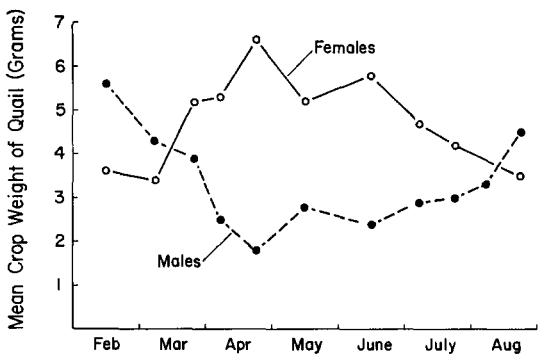

FIGURE 9. Crop weights of California Quail through the breeding season of 1967.

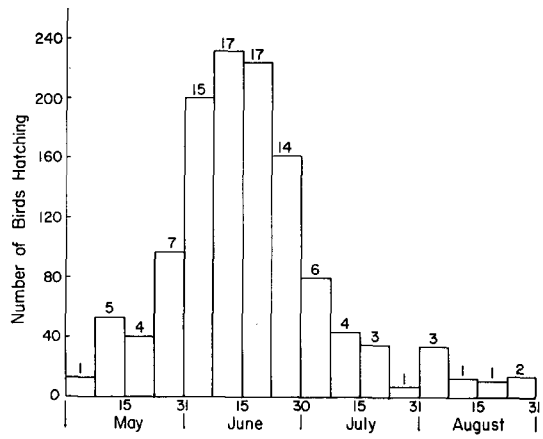

FIGURE 10. Distribution of hatching calculated by backdating from the age of broods of California Quail in southeastern Washington during 1967. (Numbers above columns indicate number of broods.)

California Quail from development of the primary wing feathers. His technique is accurate to within 4 days up to the age of 70 days and to within 9 days up to 125 days of age. The peak of hatching could be estimated, therefore, to within the nearest week. The distribution of hatching calculated by backdating from the ages of broods for California Quail on the study area during 1967 is shown in figure 10. The earliest hatching record was May 1, and the latest was August 23. June was the peak of hatching, with an estimated 66 per cent of all young being hatched during this month. Hatching declined slowly through July and August; these records probably represent renesting attempts.

The average clutch size of California Quail has been reported as 13.7 eggs in New Zealand (Williams 1967) and 14.0 eggs in California (Lewin 1963). Both of these studies were carried out over a period of 3 or 4 years, and clutches were averages for observations made throughout the laying season. By use of Lewin's data and table 3, a mortality of 12.1 per cent is estimated for quail on the

TABLE 3. Brood sizes according to age in California Quail of Southeastern Washington during 1967.

Approximate brood age	No. broods observed	Brood size Mean ± SD
4 weeks or less[a]	11	12.3 ± 3.24
6 weeks or less[a]	24	12.0 ± 2.32
8 weeks or less[b]	46	11.9 ± 3.83
10 weeks or less[b]	35	11.2 ± 2.25
12 weeks or less[b]	14	11.0 ± 2.21
15 weeks or less[b]	5	10.4 ± 2.00

[a] Includes only those broods thought to contain a complete complement of chicks.
[b] Computed for all broods observed.

study area during the first four weeks of life. Mortality was 3.3 per cent between 4 and 8 weeks of age; 7.6 per cent between 8 and 12 weeks; and 5.5 per cent between 12 and 15 weeks. Although the first four weeks of life appear to be the most critical, mortality for the present study was very low in comparison with Williams' (1957) figures. There was an estimated 25.8 per cent mortality (74.2 per cent survival) through the first 15 weeks of life for quail in the present study.

DOUBLE BROODS?

Evidence for double broods has been published for both captive and wild California Quail. McMillan (1964) witnessed early broods being reared by male California Quail only, while the remainder of the adult population continued to nest and rear additional broods. Francis (1965) observed this happening with two captive female California Quail and their mates. Additional evidence suggesting a stimulus for rearing double broods was found in the present study. Of 35 broods observed during June and July, 29 per cent were being reared by males only, 14 per cent by no parent, and 54 per cent by both parents. During August and September, 17 per cent of 62 broods were being reared by males only, none of the broods by no parent, and 81 per cent by both parents, indicating either that there was high early female mortality or that early broods were delegated to males while females attempted to hatch and rear a second brood. Seemingly, more female mortality would have occurred during the late part of the breeding season, so that percentages would be reversed. More convincing evidence was obtained with collection of females no. 76 and 85 on 11 and 27 June 1967, respectively. Both of these females were mated, were accompanied by a three- to four-week-old brood, displayed a conspicuous brood patch, and contained ovaries and oviducts in laying condition. The ovaries weighed 10.0 and 1.5 g and the oviducts 5.7 and 5.0 g, respectively. These findings suggest that these females had hatched the first brood and were about to attempt a second clutch of eggs. Whether double broods are ever hatched by California Quail in Washington is not certain, but obviously the potential for raising double broods exists among these birds.

POSTNUPTIAL MOLT

Since the molting of all other feather tracts is completed within the span of time required for the replacement of the 10 primaries, the stages of primary replacement are an accurate indication of postnuptial molt (Genelly 1955). Information on the postnuptial molt was, therefore, obtained from the wings of quail collected during the latter part of the breeding season and through the hunting season. Males began the postnuptial molt in mid-June and completed it in mid-October (fig. 11). Females began to molt about one month later (mid-July) and finished during the first part of November. The phenology and duration of the postnuptial molt of California Quail in Washington is like that of California birds as described by Genelly (1955) and Raitt (1961). Molting was much less synchronous among females than among males, presumably because of the frequent occurrence of renesting attempts which retard the molt (Genelly 1955). Convergence of the molt curves indicates that females molted faster once the molt had begun. Additional evidence of rapid progress of molting is the fact that many females exhibited several successive growing primaries. A similar lag in the postnuptial molt of female gallinaceous birds has been reported by Kabat et al. (1950) for the Ring-necked Pheasant. They found that individual hens molt at the same time as do the chicks; hence the hens do not begin to molt until after the brood hatches. Indications of this phenomenon have been reported for California Quail by Genelly (1955) and Raitt (1961) and for Gambel Quail by Raitt and Ohmart (1966). If California Quail molt one primary weekly, as do pheasants, the postnuptial molt for females does not begin until a short time after the clutch has been hatched. Young collected with females in the present study were all older than the length of time it would have required for the females

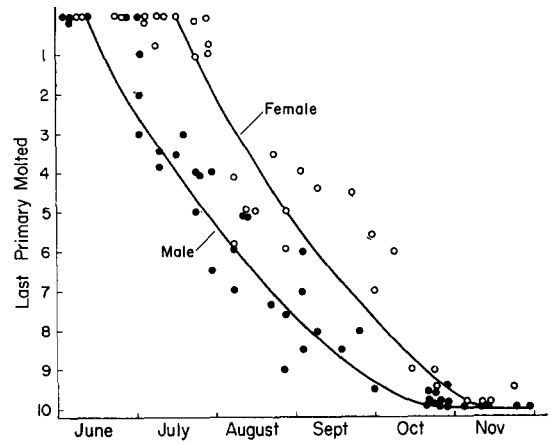

FIGURE 11. Postnuptial molt in California Quail from southeastern Washington during 1967.

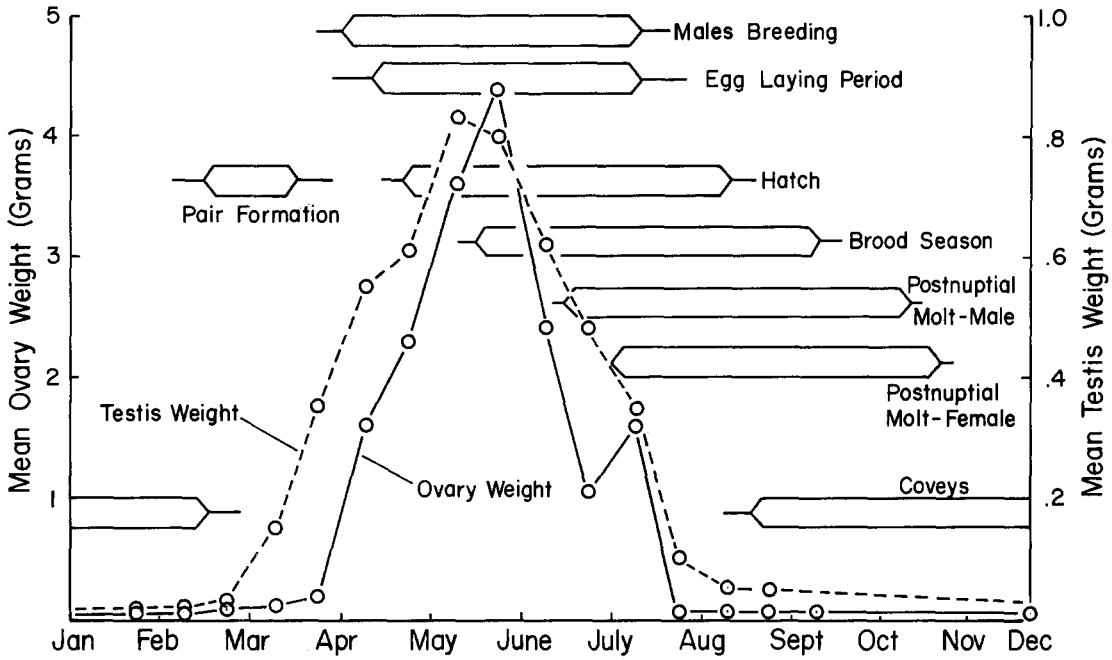

FIGURE 12. Breeding phenology of California Quail in southeastern Washington during 1967.

to molt the number of primaries already molted.

The breeding phenology of California Quail in southeastern Washington for 1967 is shown in figure 12. Time relationships of gonadal activity, social organization, laying, hatching, and molt can easily be determined from this figure.

SUMMARY

Research on the ecology and reproduction of California Quail in southeastern Washington was conducted from February 1967 until January 1968. The annual cycle of gonadal activity, body weight, and molt was studied. The left testis of males was studied histologically, and statistical treatment was applied to cell counts taken on these tissues.

Recrudescence of testes began in early March and was completed in May. Increase in size and activity of the ovaries and oviducts started in late March, laying in early May. Recrudescence of the oviduct was more rapid than that of the ovary.

Gonadal regression began in late June for both sexes, but the time of onset of regression was much more variable for females. Laying females were found as late as 29 July. Breeding condition for males, as determined histologically, persists a month after regression begins. The hatching distribution was calculated by backdating from the age of juveniles. The length of the hatching period was approximately 110 days, the peak occurring during June.

Variation in body weight of male and female quail during the breeding season was correlated, in part, with food consumption as evidenced by crop weights upon collection. Males were heavier than females during the non-breeding season, but females were heavier during the breeding season. There was a pronounced weight loss among females following laying and incubation. Sex and age ratios indicate that females suffered high mortality during the late part of the breeding season. This differential mortality among females during the breeding season probably leads to the 120:100 sex ratio favoring males.

An analysis of variance was employed to analyze statistically the testicular histology of California Quail. The difference between the mean testicular histology of adult quail and that of immature quail during the height of the breeding season was not statistically significant. Although male quail that were rearing a brood showed tendencies for faster testicular regression than males not rearing a brood, there was no statistically significant difference between the mean testicular histologies of the two groups.

Evidence for a tendency to produce double broods was found during this study, but whether double broods are ever raised by

California Quail in southeastern Washington is not known. The phenology of the postnuptial molt was very similar to that reported in other studies of this species.

ACKNOWLEDGMENTS

Numerous individuals, all of Washington State University, contributed to the project. I am sincerely grateful to I. O. Buss, Department of Zoology, who directed the study and provided counsel and editorial assistance. Acknowledgment is made to V. Schultz, Department of Zoology, and T. S. Russell, Statistical Services, for statistical and editorial suggestions. Acknowledgment is also made to R. Daubenmire, Department of Botany, and J. R. King, Department of Zoology, for their advice and editorial help. Appreciation is expressed to Washington State University for financial assistance through an NDEA Fellowship (17A 7102 Project 5400).

LITERATURE CITED

BAKER, J. R. 1938. The relation between latitude and breeding seasons in birds. Proc. Zool. Soc. London 108A:557–582.

BUSS, I. O., AND E. S. DZIEDZIC. 1955. Relation of cultivation to the disappearance of the Columbian Sharp-tailed Grouse from southeastern Washington. Condor 57:185–187.

EMLEN, J. T., JR. 1940. Sex and age ratios in survival of the California Quail. J. Wildl. Mgmt. 4: 92–99.

FISHER, R. A., AND F. YATES. 1949. Statistical tables. Hafner Publ. Co., New York.

FRANCIS, W. J. 1965. Double broods in California Quail. Condor 67:541–542.

GENELLY, R. 1955. Annual cycle in a population of California Quail. Condor 57:263–285.

GULLION, G. W., AND A. M. GULLION. 1961. Weight variations of captive Gambel Quail in the breeding season. Condor 63:95–97.

HAMILTON, M. 1957. Weights of wild Bobwhites in central Missouri. Bird-Banding 28:222–228.

KABAT, C., R. K. MEYER, AND R. L. HINE. 1956. Seasonal variation in stress resistance and survival in the hen pheasant. Wisconsin Conserv. Dept., Tech. Bull. no. 13.

KABAT, C., D. R. THOMPSON, AND F. M. KOZLIK. 1950. Pheasant weights and wing molt in relation to reproduction with survival implications. Wisconsin. Conserv. Dept., Tech. Wildl. Bull. no. 2:1–26.

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

KRUMREY, W. A., AND I. O. BUSS. 1969. Observations on the adrenal gland of the African elephant. J. Mammal. 50:90–101.

LEWIN, V. 1963. Reproduction and development of young in a population of California Quail. Condor 65:249–278.

MACKIE, R. J., AND H. K. BUECHNER. 1963. The reproductive cycle of the Chukar. J. Wildl. Mgmt. 27:246–260.

MCMILLAN, I. I. 1964. Annual population changes in California Quail. J. Wildl. Mgmt. 28:702–711.

MEYER, R. K., C. KABAT, AND I. O. BUSS. 1947. Early involuntionary changes in the postovulatory follicles of the Ring-necked Pheasants. J. Wildl. Mgmt. 11:43–49.

NAGRA, C. L., AND I. O. BUSS. 1959. Change in body weight associated with onset of ovarian recrudescence and oviposition in pheasants. Condor 61:348–350.

RAITT, R. J., JR. 1961. Plumage development and molts of California Quail. Condor 63:294–303.

RAITT, R. J., AND R. E. GENELLY. 1964. Dynamics of a population of California Quail. J. Wildl. Mgmt. 28:127–141.

RAITT, R. J., AND R. D. OHMART. 1966. Annual cycle of reproduction and molt in Gambel Quail of the Rio Grande Valley, southern New Mexico. Condor 68:541–561.

SERVENTY, D. L., AND A. J. MARSHALL. 1956. Factors influencing testis coloration in birds. Emu 56:219–222.

SEUBERT, J. L. 1952. Observations on the renesting behavior of the Ring-necked Pheasant. Trans. N. Amer. Wildl. Conf. 17:305–329.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

STORER, T. I., R. P. CRONEMILLER, E. E. HORN, AND B. GLADING. 1942. Studies on valley quail. California Agr. Sta. Bull. 663:130–135.

SUMNER, L., JR. 1935. A life history study of the California Quail, with recommendations for its conservation and management. California Fish Game 21:167–256.

WARREN, D. C., AND R. M. CONRAD. 1939. Growth of the hen's ovum. J. Agr. Res. 58:875–893.

WILLIAMS, G. R. 1952. The California Quail in New Zealand. J. Wildl. Mgmt. 16:460–483.

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.

WILLIAMS, G. R. 1963. A four-year population cycle in California Quail, *Lophortyx californicus* (Shaw) in the South Island of New Zealand. J. Anim. Ecol. 32:141–159.

WILLIAMS, G. R. 1967. The breeding biology of California Quail in New Zealand. Proc. New Zealand Ecol. Soc. 14:88–99.

Accepted for publication 18 August 1969.