

ANNUAL CYCLE OF REPRODUCTION AND MOLT IN GAMBEL QUAIL OF THE RIO GRANDE VALLEY, SOUTHERN NEW MEXICO

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Studies of seasonal cycles in various aspects of the biology of wild-bird populations are necessary for understanding the ecology of particular species. Such studies also may yield results of general interest, indicating the nature and variety of adaptations to various climatic regimes and revealing something of underlying physiological interplay among environmental stimuli, endocrine activity, gametogenesis, molts, and behavior.

Relevant to these objectives the annual cycle of populations of Gambel Quail (*Lophortyx gambelii*) in the Rio Grande Valley of southern New Mexico appeared interesting in several respects. The ecology of the species as a whole is relatively poorly known. Recent investigations have been concerned with population dynamics in southern Nevada (Gullion, 1956a, b), with population dynamics, food habits, and influence of rainfall and diet on reproduction in southern Arizona (Sowls, 1960; Hungerford, 1962, 1964), and with general ecological distribution and habitat relationships (Gullion, 1960). Basic detailed information on cycles of gonadal activity, molt, and behavior for the species and on all aspects of the ecology of populations in the eastern portion of its range is almost entirely lacking in the published literature.

The several detailed studies of annual cycles in other gallinaceous species provide a background against which results for Gambel Quail can be compared, thus enhancing the probability of recognizing significant generalizations.

With these goals in mind such a study was carried out from March 1959 through October 1961. Results pertaining to gonadal, molt, and behavioral cycles and the relationships among them will be discussed in this report.

STUDY AREA AND POPULATIONS

The populations studied inhabit the edges of a portion of the Rio Grande Valley in the vicinity of Las Cruces and University Park, Dona Ana County, New Mexico (32° 20' N, 106° 45' W). This portion is known locally as the Mesilla Valley. Most of the rural portion of the valley proper is cultivated; cotton is the principal crop, but alfalfa fields, truck farms, and pecan orchards occupy considerable areas.

Suitable habitat for quail is found in restricted riparian "bosques" dominated by tall mesquite (*Prosopis juliflora*), tornillo (*Prosopis pubescens*), and introduced tamarisk (*Tamarix pentandra*), with shrubs in openings and at edges including mesquite, chamiso (*Atriplex canescens*), arrowweed (*Pluchea sericea*), wolfberry (*Lycium* spp.), *Rhus trilobata*, and jimmyweed (*Haplopappus heterophyllus*). Other quail habitats occur at various places along some of the numerous irrigation canals, where their banks are not cleared or where adjacent, usually small, parcels of land are left uncultivated, and at the margins of the valley where cultivated fields meet uncultivated desert "mesa" slopes or, especially, arroyos. The vegetation in habitats along the canals is variable but is generally a lower, more open, poor representation of the river bosques with an important addition of dense clumps of Johnson grass (*Sorghum helapense*); at the valley edges low-growing mesquite and chamiso are dominant with variable numbers of mesquite and tornillo of arboreal stature and with clumps of Johnson grass on ditch banks along perimeters of fields. In all habitats annual forbs, especially Russian thistle (*Salsola kali*), *Verbesina encelioides*, and others, of the families Asteraceae, Chenopodiaceae, and Amaranthaceae, are important

and abundant. Cottonwoods (*Populus fremonti*) are scattered throughout the area, but their numbers have been so greatly reduced through cutting and burning that they can have but little influence on quail.

The climate of the area is arid, with a mean annual precipitation of 7.93 inches, most of it as heavy rain in the summer. Annual variation in precipitation is considerable; in 1959 the weather station at University Park recorded 5.93 inches; in 1960, 7.73 inches; and in 1961, 10.06 inches. Temperature variation is moderate, although maxima in summer are consistently high. The highest temperature recorded during the study was 107° F on 21 June 1960. Maxima in 1959 and 1961 were 102° and 101° F, respectively. Nights become frost free in late March or early April (last frosts occurred 22 March 1959; 3 April 1960; and 9 April 1961) and remain so until late October or early November (first frosts occurred 6 November 1959; 31 October 1960; and 3 November 1961), giving an annual growing season of more than 200 days. The combination of low humidity, high temperatures, and moderately heavy winds produces annual evaporation rates of more than 90 inches.

Organisms living under these climatic conditions usually face difficult problems of water economy. However, for the quail under study the problems are alleviated by the fact that free water is available throughout much of the year. The water in most habitats is provided through irrigation, which insures the availability of water during the breeding season when quail needs are probably most critical.

Although quail are abundant in the valley, the encroachment of man's activities has resulted in fragmentation of habitat. It was therefore not feasible to collect the large samples necessary for this study from a single, continuous population. The principal area of collection and study was a band of mesquite-chamiso vegetation between cultivated fields and the edge of the "east mesa" south of University Park on and around the former site of Fort Fillmore. Three other main areas were utilized in order to prevent drastic seasonal reduction in density in any one location; these other sites included one at the eastern edge of the valley near Dona Ana and two at the western edge of the valley near La Mesilla. A few other sites were used to a minor degree, principally during the summer when quail were difficult to trap. All locations are in the valley proper but on its edges, and lie within a radius of seven miles. In each area the quail had available for feeding and watering either irrigated fields or mesic bosques. All areas were subject to hunting. Thus, although collecting and observation were not carried out in a single, restricted area, the quail included were all living under similar environmental conditions.

METHODS

Most of the specimens for this study were trapped alive using poultry-mesh boxes with funnel-shaped entrances and with grain for bait. Trapped birds were brought to the laboratory, killed by thoracic compression, and weighed; various portions were dissected and preserved for later study. On all birds the medial portion of the back was preserved in Bouin's fluid with sexual organs and adrenal glands intact. Both thyroid glands were dissected from most specimens and were preserved in Bouin's fluid also. From molting birds one wing was preserved and dried. Study skins were prepared from several selected molting birds.

Trapping was impractical during the regular quail-hunting season, and collections during these periods were therefore made by shooting. Shot specimens were taken as soon as possible to the laboratory and treated as just described.

Trapping and shooting yielded a total of 420 specimens. An additional 155 were trapped but not killed.

In early fall, trapping success was very high, particularly for juveniles. Many of these were banded and released after examination of plumage development. Recapture of these marked individuals provided additional information on the timing of the postjuvencal molt.

Preserved organs were taken out of Bouin's fixative, usually within a week after death, washed, and stored in 70 per cent ethanol. Weights and measurements were all taken from these stored specimens. Organs to be studied histologically were embedded in paraffin and prepared by conventional methods. Additional descriptions and discussion of methods used in specific phases of the study will be given subsequently.

Most observations on behavior were made while visiting traps. Although somewhat unsystematic, these observations were sufficient to document the timing of principal seasonal changes in behavior patterns. More intensive observations were made, especially in spring 1961, on behavior of a covey inhabiting the edges of a portion of the campus of New Mexico State University.

The nature and timing of seasonal changes during at least a major portion of the study period were documented for gonads, molts, body weights, and a number of aspects of behavior. Results on each of these phases of the annual cycle will be discussed in turn. Information on population parameters and on thyroid and adrenal cycles will be published separately.

TESTIS CYCLE

Methods. Testes from 198 males were utilized in the study; in nearly all cases only the left testis was studied. In a few birds this one was damaged by shot, and the right one was used. Length and largest diameter of all testes were measured to the nearest 0.1 mm with a dial caliper; weight to the nearest 0.1 g was taken on a torsion balance. Lewin (1963:252) showed that testes of California Quail shrink a maximum of 3 per cent in fixative. Efforts were made to minimize and standardize the time between removal from preservative and taking of measurements. In view of the great seasonal variation in testis size, errors due to preservation are almost certainly insignificant. Several transverse sections 10 microns in thickness were cut through the center of each testis. These were stained in Harris' hematoxylin and counterstained with eosin.

Results. As is usual in birds of temperate regions, gonads of males in these quail populations undergo definite seasonal changes in size and activity. Figure 1 illustrates the cycle in size.

Only data for length are presented, although both length and weight were measured. The two are highly correlated, and length is more useful for comparison with results of other studies. Data from the three breeding seasons, 1959, 1960, 1961, are combined because no differences are discernible. Among full-grown males of different ages no differences due to age are apparent. On a population basis, increase in testis size during recrudescence was both rapid and uniform. Both weight and length began to increase markedly before the end of February. Full testis size was reached as early as mid-April in some birds and by the end of April in all birds. The first indications of regression in size occurred on 30 June 1960 and 7 July 1961. By the end of July testes of all males were less than full size. Return of testes of all birds to winter size was not completed until early November. Decrease in size was both more gradual and more variable than increase.

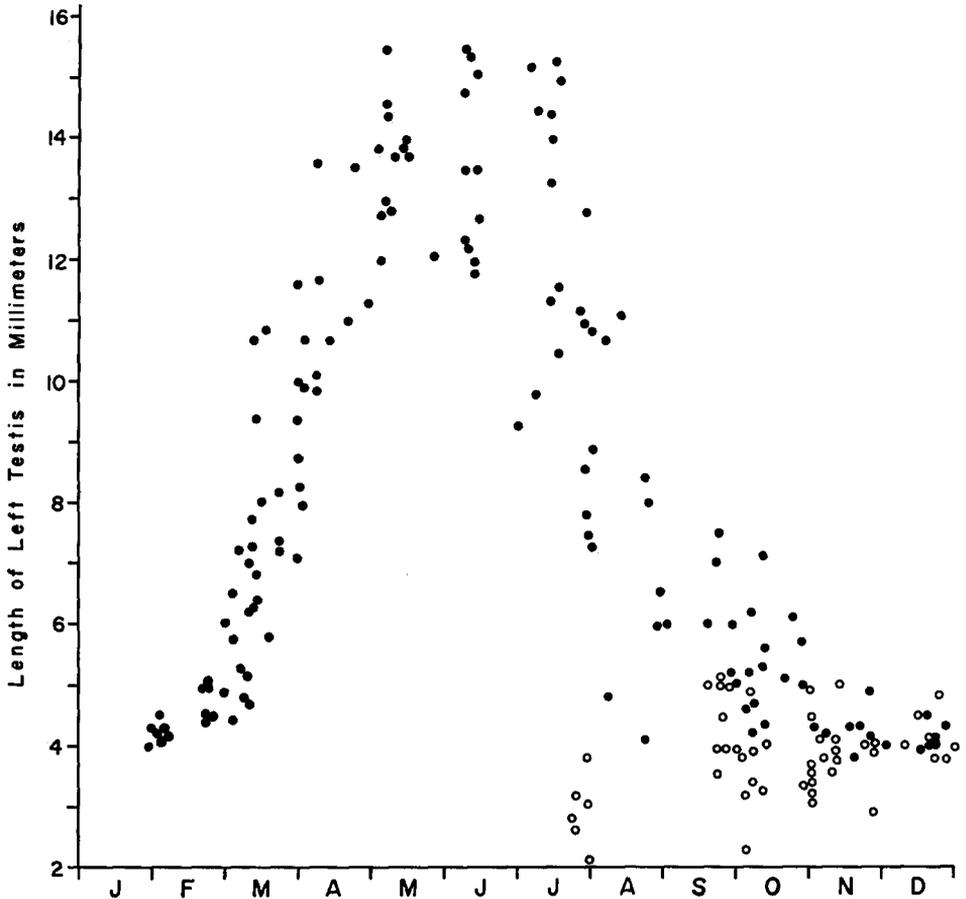


Figure 1. Seasonal changes in testis length in Gambel Quail. Solid dots indicate adults; open circles indicate juveniles.

Histological changes in the cycle of spermatogenesis were very similar to those described by Lewin (1963:252-255) for California Quail. For facilitation of comparisons, the same designation of stages in the cycle is used in this study. Full description of the various stages would be unnecessarily repetitious of Lewin's presentation, but a summary (table 1) of characteristics of the stages is provided for reference. It should be emphasized that these stages are arbitrary subdivisions of a continuous process; however, it was not difficult to assign individual testes to one of the several stages except in the late breeding season when the initial stages of regression are difficult to detect.

Seasonal occurrence of these stages is depicted in figure 2. The pattern is similar to that already described for size, and the two are highly correlated. However, range in size of testes of a particular stage overlaps slightly with those of adjacent stages in most cases. Testes of stages 2 and 3 overlap to a considerable degree, and those of stage 5 and early regression are very similar in size. Onset of testicular recrudescence in spring is readily apparent from histological characteristics in some birds collected

TABLE 1
RÉSUMÉ OF MAJOR HISTOLOGICAL CHARACTERISTICS OF TESTICULAR STAGES IN GAMBEL QUAIL

Stage	Range of tubular diameters, microns ^a	Lumina	Tubular histology	Interstitial
1	32-41	usually present; small	mainly spermatogonia; few primary spermatocytes	abundant, especially connective tissue; often heavy pigment
2	62-72	generally absent	spermatogonia; primary spermatocytes in synapsis	moderate; Leydig cells prominent; moderate pigment
3	83-92	present; small	spermatogonia; primary and secondary spermatocytes	reduced but still continuous; Leydig cells prominent; pigment sparse
4	112-156	large	spermatogonia, spermatocytes, spermatids, some spermatozoa in bundles	generally more restricted, discontinuous; pigment very sparse
5	154-236	large; contain spermatozoa	all spermatogenic stages	definitely discontinuous; all elements sparse
Regression				
Early	147-183	some large, containing detritus; some collapsed	becoming disorganized, especially near lumina	slightly increased fibrous connective tissue and pigment
Medium	76-108	usually occluded	highly disorganized	moderate fibrous connective tissue, vascularization and pigment
Late	61-81	variable	spermatogonia in rows at periphery; centers still disorganized	as in stage 1, except connective tissue more fibrous

^a Ranges of mean diameters (N = 10) for 4 or 5 typical specimens in each stage.

as early as the first week in February, but increase in size is not obvious until later in February.

The most significant facts revealed by the study of testes of birds of breeding age include the previously mentioned uniformity in annual onset of recrudescence in early February and the occurrence of full sexual activity in a large proportion of males from the beginning of April until past mid-July.

A small number of immatures exhibited spermatogenic activity in the autumn, but this activity failed to reach even full stage 2. Lewin (1963:256) found no indication of autumnal spermatogenesis in juvenal California Quail.

Discussion. The testis cycle in these Gambel Quail closely resembles that in the California Quail near Berkeley, California, reported by Lewin (1963). The correspondence of histological stages has already been mentioned; in the rapid, synchronous recrudescence and more gradual, irregular regression the two species are also similar, although some aspects of the timing are different.

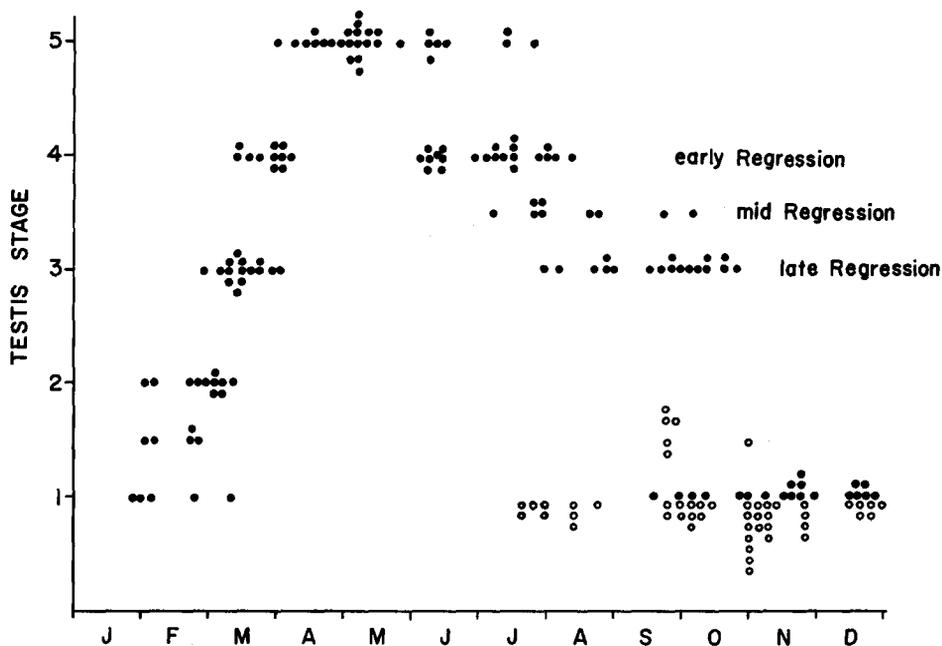


Figure 2. Annual cycle of histological stages of testis activity in Gambel Quail. Solid dots indicate adults; open circles indicate juveniles. Stage numbers refer only to recrudescence. See table 1.

Consideration of the timing of the breeding season will be deferred until other aspects of the cycle have been discussed; however, it may be pointed out here that the period of approximately 15 weeks of full production of spermatozoa (stage 5) by males in these Gambel Quail populations is longer than reported for two other small gallinaceous birds in North America. Lewin's data for California Quail (1963: fig. 2) indicate maintenance of a comparable stage for less than 12 weeks. For the Chukar (*Alectoris graeca*) in Washington, Mackie and Buechner (1963) did not provide histological data, but their information on size and egg dates indicates a period not greater than Lewin found. On the other hand, Hiatt and Fisher (1947) report fully active testes in Ring-necked Pheasant (*Phasianus colchicus*) populations in Montana for a period of 19 weeks.

FEMALE REPRODUCTIVE CYCLE

Methods. Preserved ovaries from 184 females were weighed to the nearest milligram on a Roller-Smith balance. Largest diameter of the largest ovarian follicle was measured with a dial caliper on most ovaries. Oviducts were likewise weighed, after removal of any contained ova. The general stage of development of incubation patches was noted at time of sacrifice of all females bearing them.

Serial sections were made of several ovaries in order to investigate the possibility of counting postovulatory follicles. However, as Lewin (1963:257-258) found in California Quail, such follicles apparently regress rapidly, and it was not possible to identify older ones with sufficient confidence, and thus to make reliable counts. Microscopic examination did aid in determination of whether ovaries of intermediate size were regressing or recrudescing.

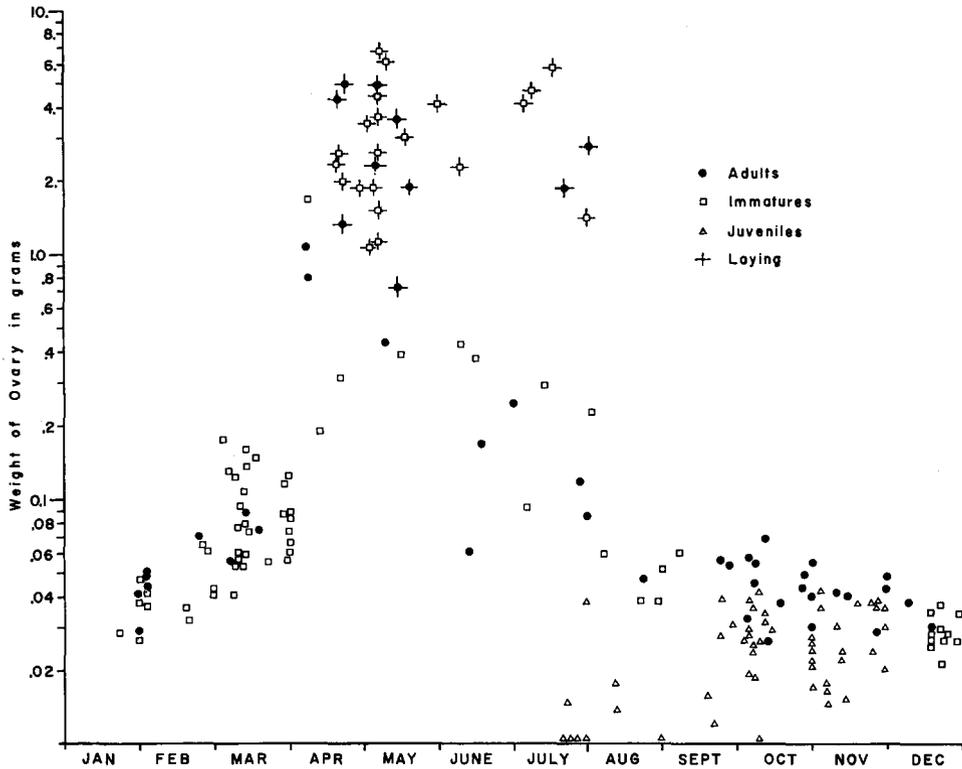


Figure 3. Seasonal changes in ovary weight in Gambel Quail.

Results. Weights of ovaries by date are plotted in figure 3, those of oviducts in figure 4. As with testes, no trenchant annual differences are apparent, and data for the three years are pooled. The symbols used by Lewin (1963) are also used in these graphs in order to facilitate comparison. Changes in weight of ovaries and oviducts show similar patterns, and the two appear to be equal as indicators of reproductive state. Data for diameters of follicles are not presented, but seasonal changes resemble those of ovaries. Before recrudescence, ovaries and oviducts of immature females (full-grown birds in their first year) were smaller than those of adults. However, onset of rapid recrudescence occurred at about the same time in both groups, and, although immatures appeared to lag behind adults during recrudescence, they reached laying condition only slightly later than did adults. Lewin (1963: figs. 9, 12) found a similar pattern in California Quail; Mackie and Buechner (1963: table 3) also found quiescent ovaries and oviducts in immature Chukars to be smaller than in adults.

Vernal recrudescence in female reproductive organs was rapid. It began in late February and early March, about two weeks later than in males, and the earliest laying hen was collected on 19 April 1961, 19 days later than the earliest fully active testis. On a population basis, recrudescence of ovaries and oviducts was more variable than was that of testes, perhaps largely because of the differences between age groups in females. Ovulating females were collected from 19 April to 2 August, indicating

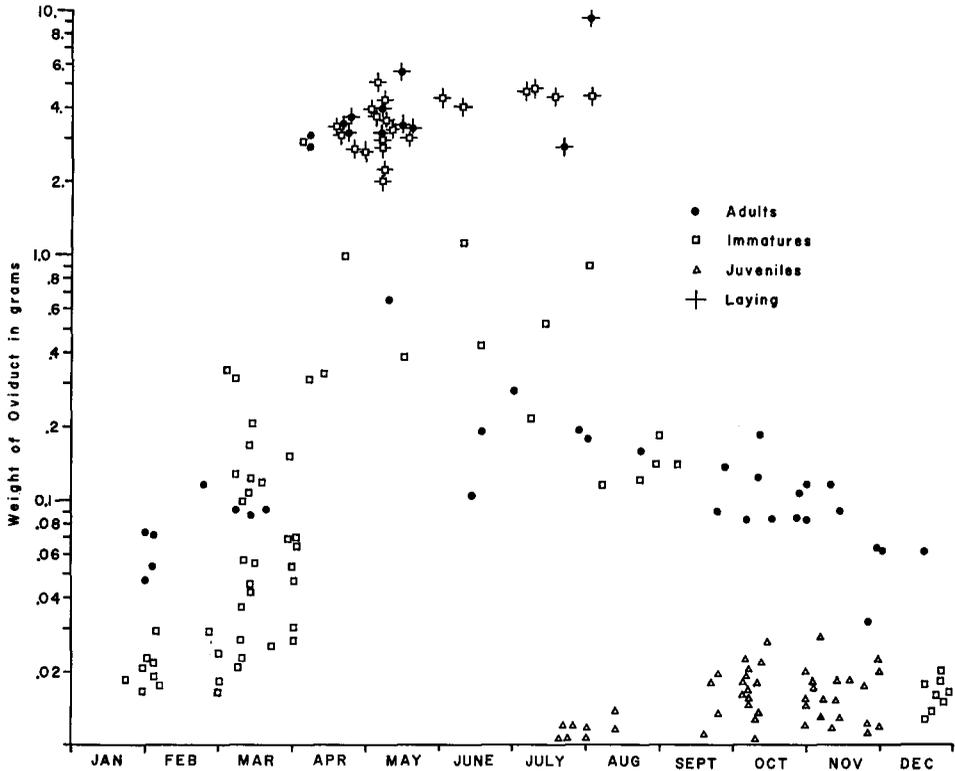


Figure 4. Seasonal changes in oviduct weight in Gambel Quail.

a laying season of about 15 weeks. Hatching dates obtained by back-dating from captures of juveniles (to be discussed in more detail in a subsequent section) indicate a similar average laying season.

Regression of reproductive organs in females was even more variable than in males; it began as early as 15 May 1959, 9 June 1960, and 9 May 1961; but, as mentioned above, some individuals were still laying in late July and early August. Both regression and recrudescence of the ovary and oviduct in individuals must occur rapidly because very few were found in intermediate stages.

Occurrence of incubation patches added little knowledge to that provided by ovaries and oviducts. All females with obviously regressing ovaries and oviducts possessed incubation patches, and the stage of development of these patches was correlated with the stage of regression of reproductive organs. The several birds still ovulating late in the season showed definite signs of incubation-patch development, but no such development was noted in ovulating birds collected early and in the middle of the season (April, May). No males with incubation patches were noted.

Discussion. The similarity of these cycles in female Gambel Quail to those reported by Lewin (1963) for California Quail is great, as in males. In fact, the species differences in timing of recrudescence noted for males are not apparent in females. However, the longer period of full gonadal activity in Gambel Quail males was matched by a longer one in females. In both species ovulating females were first captured in the second half of April, but in the present study the latest dates of such

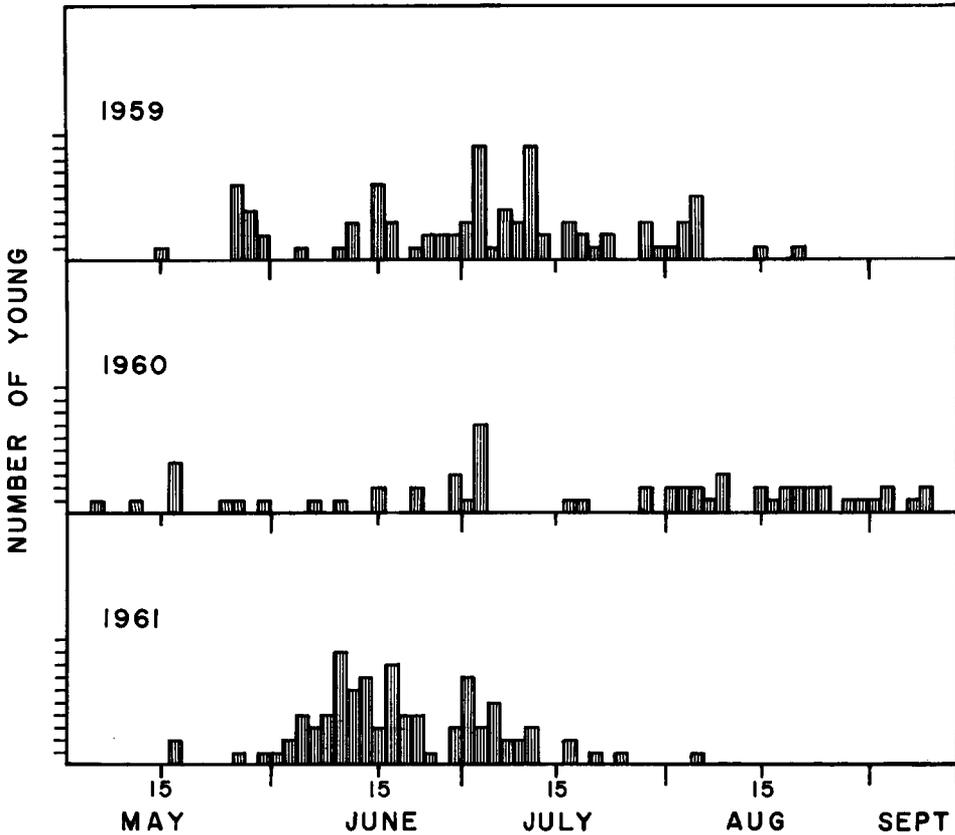


Figure 5. Frequency distribution of hatching dates of Gambel Quail. Each unit on the time scale represents two days.

captures were in early August, versus mid-June for the other species (Lewin, 1963: fig. 5). Another difference between the species is the greater variability of the onset of regression in the Gambel Quail; this greater duration is perhaps related to the deferred complete cessation of ovulation.

The long period of ovulation in the population compared with the early ovarian regression and incubation-patch development of some individuals suggests that there may be time available for females producing early clutches to produce a second clutch in the same year. Gullion (1956b) has provided evidence of double-brooding in Gambel Quail in Nevada. The method of sacrificing individuals used in this study is unlikely to produce definitive evidence on this point, but the extended hatching season described below is suggestive of two broods. At least the long periods of breeding activity and hatching indicate that these quail are able repeatedly to exercise the well-known propensity of gallinaceous birds to renest following reproductive failure.

HATCHING DATES

The capture of juvenal birds provided additional data on the reproductive cycle. The age of each trapped juvenile was estimated by use of criteria based on stage of

molt. Hatching dates were then deduced by back-dating. The age criteria were developed for California Quail by Raitt (1961). But comparisons of plumage development showed the two species to be virtually identical, and it is therefore believed that the use of age criteria based on California Quail is justifiable. Absolute ages estimated by plumage criteria are, of course, only approximations; but they are used in this study primarily in conservative ways, to indicate total length of hatching season and to compare different seasons.

Hatching dates obtained in this way for the three seasons are plotted in figure 5. The durations of the hatching seasons—98, 128, and 81 days in 1959, 1960, and 1961, respectively—correspond fairly well with the laying season of 108 days as determined from pooled data from adult ovaries. An additional step in back-dating to obtain laying dates gives dates of onset and cessation of laying that also agree in general with data from ovaries.

As stated previously, the ovarian cycles of different years showed few differences. However, difficulties in collecting females within the breeding season resulted in rather small samples and in an unfortunate complementarity among years in dates of capture. These deficiencies in sampling could have obscured differences in timing among years. The larger amount of data from hatching dates would appear to provide the best basis for year-to-year comparisons. For California Quail, Raitt (1960) and Lewin (1963) have utilized hatching dates for such comparisons. Comparison of years in figure 5 reveals only slight variation in dates of the earliest hatch; these are probably statistically insignificant. Thus neither ovaries nor hatching dates reveal the sort of variation among years in initiation of full breeding activity that Raitt and Lewin found separately for California Quail. Whether the situation in these three years is typical or whether laying and hatching may be delayed by unfavorable weather is impossible to determine with the data at hand. Dates of late hatches varied considerably, and the late dates of 1960 are correlated with the capture of ovulating hens in August of that year. So many environmental variables might conceivably influence the later extent of hatching that to discover those responsible for the variation among the three years seems impossible. It does appear that temperatures late in the hatching season were not the cause, for extreme temperatures did not occur until much later in the year. The absence of normal heavy rains late in the hatching season in 1960 may have favored later nesting effort.

BEHAVIORAL CYCLE

The study of behavior in this research was directed mainly toward determining the timing of well-marked and well-known changes in behavior in order to complement and reinforce information on other phases of the cycle. The accounts of Gorsuch (1934), Gullion (1956a), Leopold (1959), Miller and Stebbins (1964), and of several earlier students provide general outlines of the seasonal changes in social behavior in Gambel Quail.

These sources plus early work in this study indicate that the annual cycle in social behavior in Gambel Quail parallels that in its congener, *L. californicus*, as described by Sumner (1935), Emlen (1939), Genelly (1955), and Raitt (1960), among others. The first behavioral indication of the onset of the breeding is increased hostile interaction within the coveys in late winter. Throughout the spring the pair bonds are formed, and the coveys gradually dissolve as pairs become isolated from each other and as mutually intolerant, unmated males disperse. Throughout nearly all of the pairing and nesting season unmated males exhibit calling behavior similar to that of

such males in other quail species. In summer, as young-of-the-year begin to approach adult size, new coveys begin to form, and by late summer all birds are again in coveys.

The timing and some of the descriptive details of the events in this cycle were noted in the breeding seasons of 1959, 1960, and 1961.

Pairing and dissolution of coveys. Earliest dates of observations of pairing within coveys were on 11 March 1959, 19 March 1960, and 7 March 1961. The progress of covey break-up and behavior incident to pair formation were observed closely in a covey inhabiting an area on the edge of the New Mexico State University campus in 1961. In nearly all obvious respects this behavior closely resembled that described in California Quail by Genelly (1955) and Raitt (1960).

Hostile interactions were observed with increasing frequency as the season progressed. They usually occurred between members of the same sex, more frequently in males. The predominant form was the simple chase, but several "cockfights" were witnessed as were a few instances of the "side-by-side nudging" type of supplanting encounter. Vocalizations accompanying fighting appeared to be different from those of California Quail—for example the aggressive "squill" call was not heard—but they were not studied sufficiently to describe them accurately.

Several instances of copulation were seen, and they also resembled those of California Quail in being brief, inconspicuous, and lacking in detectable precursory displays and vocalizations. Pair formation appears to be accomplished principally through subtle interaction accompanying the frequent association of members of the opposite sexes throughout the winter and the long period of covey break-up. Except for one sort of behavior no obvious courtship or pairing behavior was noted.

A hostile interaction that may have been involved in pair formation was the chasing of a single female by several males. This type of behavior was observed on four occasions in early March. In each instance the female was chased vigorously for several seconds by more than two males. Each male appeared to take up the chase in turn, but at least twice several were chasing together. The female fled rapidly, dodging around bushes and other members of the covey and was apparently not caught. Cessation of chasing occurred as the males, apparently spontaneously, simply stopped pursuit. Accompanying this behavior in each instance were several peculiar calls, apparently given by the males. They consisted of explosive high-pitched notes interspersed by softer notes lower in pitch and longer in duration, like soft, drawn-out versions of the "cow" calls of unmated males. Similar calls were heard on another occasion in which a single male chased a female. This behavior is reminiscent of the rushing of females by courting males reported in California Quail by Genelly (1955: 267) and in Bobwhites by Stoddard (1931:17-18).

By 1 May each year the pairing process was virtually complete, and the coveys were no longer observed. After that date the largest groups of adults observed were of four individuals, two of each sex. Late observations of what might be considered coveys were of a group of 12 paired birds on 21 April 1960, and one of about 10 birds on 16 April 1959.

"Cow" calling. The crow of unmated males in this species is similar to the "cow" call reported by students of California Quail (Sumner, 1935; Genelly, 1955; and others). Gorsuch (1934:20-21) described the behavior associated with this call and believed it to be given exclusively by unmated males, as in other species of quail. Our observations support this belief.

The "cow" call may function in pair formation and is definitely associated with the season of pairing and covey dissolution, but it is treated separately here because

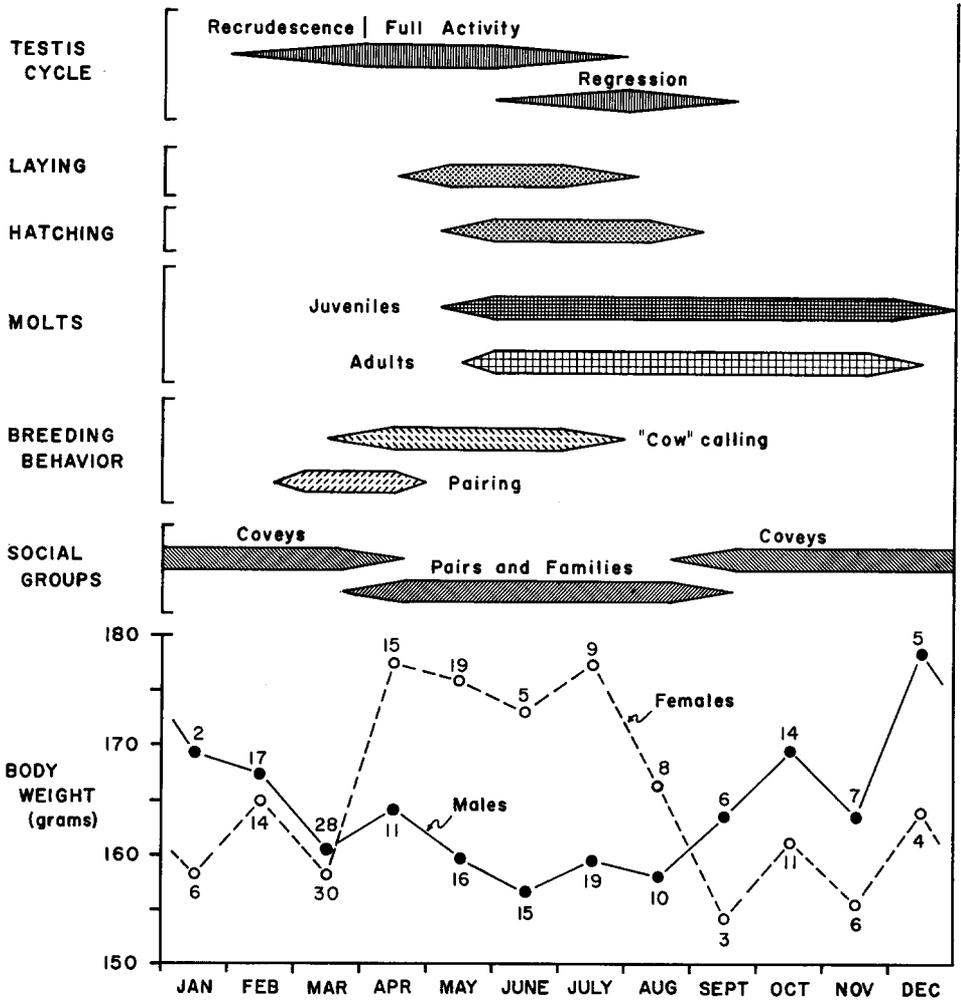


Figure 6. Mean monthly body weights of adult Gambel Quail and diagrammatic summary of timing of other aspects of the annual cycle. Numerals beside symbols indicate sample sizes.

it is unique as an obvious and well-defined behavioral indicator of reproductive status; special attention was given to the seasonal limits of "cow" calling behavior. Earliest dates on which "cow" calling was heard were 17 March 1959; 16 March 1960; and 12 March 1961. From the sporadic calling heard in March the volume of calling rose to a higher level in April, May, and early June and then declined. The latest "cow" calls heard in 1960 were on 2 August and in 1961 on 25 July. Thus, the cycle of "cow" calling closely paralleled that of the testis, merely lagging a bit at the onset in early spring (fig. 6). It also resembled the periodicity described by Genelly (1955:270) for California Quail.

Covey reformation. Coveys began to form again in September as the developing young approached full size and as gonadal activity waned. Latest observations of

pairs were made in September, but by the end of this month most of the birds were in coveys, except for a few family groups resulting from late clutches. Later observations of these families were more numerous in 1960, supporting the other indications of late hatching in that year.

Relationship to other cycles. The general timing of behavioral changes is indicated in figure 6. The correlations with cycles in other phases are obvious. The relationship between behavior and the other cycles appears to have been largely one of gonadal changes affecting behavioral changes, but there is also evidence, to be cited below, that behavior exerts an effect on timing of gonadal cycles, particularly late in the breeding season.

BODY WEIGHT

Fluctuations in body weight have been found to be correlated suggestively with reproductive activity in wild Gambel Quail by Gorsuch (1934:44-46), in captives of this species by Gullion and Gullion (1961), and in wild California Quail by Genelly (1955:283-284) and Lewin (1963:266-268). Mean monthly weights of adult males and females in this study are shown in figure 6. Variations less than about 5 g may be the result of sampling error, but general trends of body weight are apparent. The general pattern of males outweighing females during winter but surpassed by females in the laying season agrees with the results of other investigations (Genelly, 1955; Lewin, 1963), although there are temporal differences that are consistent with differences in timing of reproduction and molt. The spring decline in weight in males in this study occurred earlier, in February-March rather than in March-April, as did the onset of pairing behavior and testis recrudescence. The longer periods of elevated weight in females and depressed weight in males correspond with the extended breeding season already described. The general agreement with data of other workers, with departures matching departures in timing of reproductive activities, supports the interpretations of those cited above that changes in body weight are largely governed by reproductive behavior. Thus, reduced weight in males is probably caused by increased locomotor activity and diminished attention to feeding during pairing and care of young. Elevated weight of females is incident to laying and falls off as laying ceases and they become active in caring for young; and increase in weight in both sexes in autumn occurs because reproductive activities late in the season demand less energy and attention. The energy demands of molting appear to have little depressing effect on mean body weight.

Study of body weight of juveniles at various stages of plumage development indicates, as might be expected, that the growth of young is similar to that reported for other quails (Genelly, 1955: fig. 7, and Lewin, 1963: fig. 15, for California Quail; Wallmo, 1956: fig. 39, for Scaled Quail), full size being attained by about 120 days of age.

MOLTS

Data on the postnuptial molt were obtained from 118 adults collected in the late summer and autumn and from a few that were trapped, marked, and released. Study of postnatal and postjuvinal molts was based on 252 birds; 105 were sacrificed and 147 were marked and released. Of the latter, 48 were recaptured a total of 111 times. At each capture at least the stage of progress of molt of primaries was noted.

Since the progress of molts in general in quail can be judged well from the stage of primary replacement (see Raitt, 1961), in this study reliance was placed on indexes of molt stages based on this series of remiges. Spot checks of other tracts on

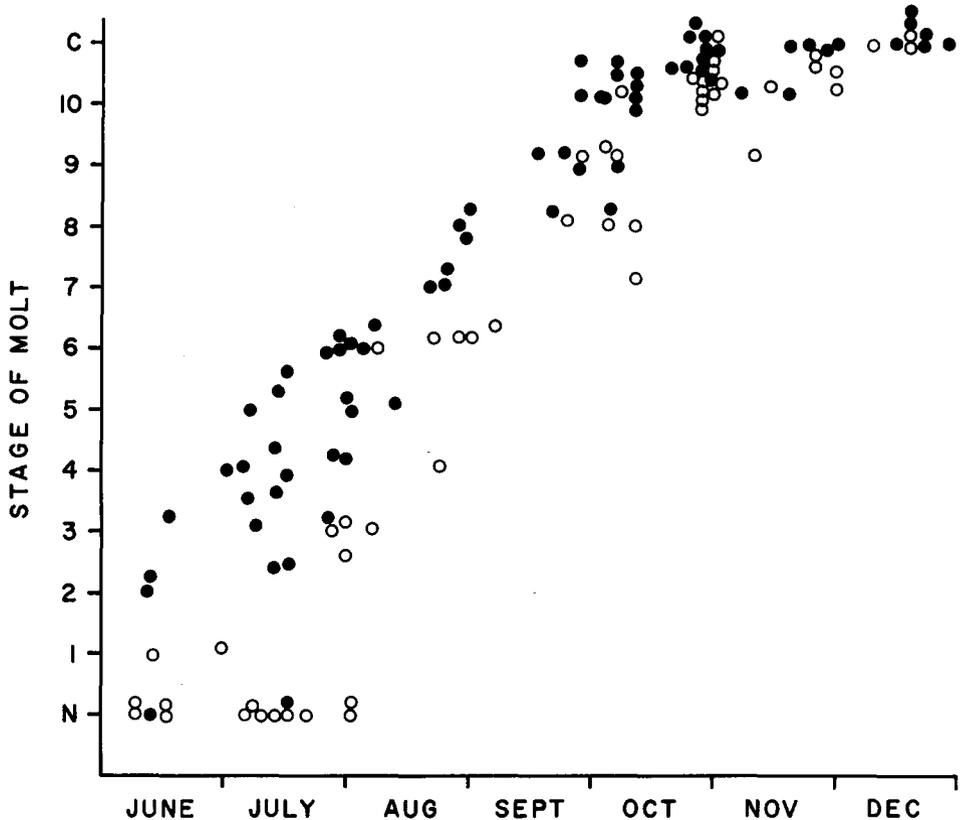


Figure 7. Timing of adult molt in Gambel Quail. Solid dots denote males; open circles denote females. The letter "N" signifies that molt had not begun; "C" signifies molt completed. Stages of molt correspond to the number of the primary last molted; substages are determined by length of the feather relative to full-grown length (see text, and Raitt, 1961).

molting adults at various stages showed no evidence of departure from the situation in California Quail and other odontophorines. In these, there is a good correlation of stage of molting in other feather series with stage of primary replacement, and virtually the entire molt is coincident with the primary molt. For juveniles more detailed study was made of molt sequences, and results will be discussed beyond; but it is pertinent to note here that primary replacement is also a reliable index in juveniles.

Annual molt. In these quail there was a single, annual, postnuptial molt; no evidence of prenuptial molting was seen. The molt stages of all birds captured during the postnuptial period are plotted in figure 7. Although repeated captures were not made of adults, the graph suggests that the molt required approximately 21 weeks in individual males, and somewhat less in females. In these features and in the general form of the scatter, these quail were very similar to the California Quail studied by Genelly (1955) and Raitt (1961). Another similarity is that females began molting later on the average than males but completed their molt very little later.

Onset of molting in the population in early June is also similar to the reports for

California Quail. However, the extension of the molting period well into December is dissimilar. That this protraction is probably due to later onset of molt in some individuals rather than to variation in duration of the molt among individuals is implied by the occurrence of birds not yet molting through July and into August. Part of the variation is due to annual variation in timing. On the average molting occurred slightly later in 1960 than in the other years.

Comparison of figure 7 with the graphs of gonad cycles (figs. 1, 2, and 3) reveals that the onset of molting in the population is concurrent with regression of gonads. This general concurrence, along with the agreement between a relatively long period of onset of both gonad regression and molt and between late breeding and late molting in 1960, suggests the possibility of a causal relationship between the two phenomena. Additional evidence is derived from comparison of molt stage and gonad stage in individual birds. Most of the adults in early stages of molt possessed regressing gonads; however, at least one molting female possessed an active ovary and an egg in the shell gland of the oviduct, and several males well along in the molt had testes in active or very early regressive stages. Furthermore, a few individuals with regressing gonads had not yet begun to molt. Thus, on an individual basis, there were three sequences: (1) molting following very soon after the beginning of gonad regression, (2) molting beginning when regression was already well under way, and (3) beginning of molt while gonads were still active. It appears, therefore, that the onset of molt and regression of gonadal activity, although generally concurrent in these Gambel Quail, are partly independent processes. It is doubtful that they are related in a directly causative manner, as seems to be implied, at least in females, for California Quail by Genelly (1955) and Raitt (1961), and for Ring-necked Pheasants by Kabat, Thompson, and Kozlik (1950). Evidence of independent timing of molt and reproductive cycles has been reported for other species by a number of other workers (*e.g.*, Marshall and Coombs, 1957; Pitelka, 1958; and Dixon, 1962).

Molts in immature birds. The sequence of molts and plumages in young Gambel Quail is like that of other North American quails. They undergo two molts before acquiring the first winter (= first nuptial or first basic) plumage; these are the postnatal molt, in which the natal down is replaced by the juvenal plumage, and the postjuvenal molt, in which the juvenal plumage is replaced by the first winter plumage. The two outermost primaries and the greater primary coverts of the juvenal plumage are not molted until the first postnuptial molt; otherwise the postjuvenal molt is complete and results in a plumage apparently identical to that of full adults.

Since this study was based entirely on wild-captured birds, data on early stages of the postnatal molt were not obtained because birds at these ages were too small to be trapped. However, the large sample of trapped individuals of various ages beyond four weeks and the repeated recapture of some of these permitted the course of the postjuvenal molt to be followed in some detail. As analyzed by methods identical with those applied to California Quail by Raitt (1961), the sequence of molting in the respective tracts and the correlation between tracts appeared to be indistinguishable in the two species. In addition, the repeated recaptures of young quail in this study made it possible to determine the time required to progress from one stage to another. A composite graph of the stage of primary molt plotted against time (method from Genelly, 1955:280, fig. 7) indicates that the postjuvenal molt in these quail had virtually the same rate and duration—19 to 20 weeks—as in California Quail. Intervals between recaptures of several banded young were checked

against the apparent intervals as indicated by age criteria for California Quail. The agreement was close, involving errors no larger than those expected in use of these criteria for wild California Quail (Raitt, 1961:300-301). However, a majority of the discrepancies were in a direction suggesting that the Gambel Quail may have required slightly longer to complete their molts. The consistent and close similarity of the postjuvinal molt in the two species is taken as justification of the use of the age criteria for California Quail in estimating hatching dates in this study (fig. 5).

Since the hatching dates were estimated from known stages of molt, they may be used in analysis of the timing of molting in the young of the population. Thus, postnatal and postjuvinal molting began earlier and extended later in 1960 than in 1959 and 1961. The period of molting among young in the population extended from the middle of May until late December. That this was a longer period than in adults was probably due to two differences: (1) that the two molts in the individual young quail require a somewhat longer period than does the individual adult molt and (2) that there was a greater synchrony in onset of molt among adults than in hatching among juveniles.

GENERAL DISCUSSION

Integration and proximate controls. The various periodic phenomena studied in these quail occur, as in virtually all temperate-zone birds, in a regular sequence, forming a single, integrated annual cycle rather than several independent cycles. Presumably because of relative freedom from exigencies of climatic extremes, the cycle (as illustrated in figure 6) gives the impression of moving at a leisurely pace; nearly the whole year is required in reproduction, with barely a month intervening between the completion of development of young produced in one season and the onset of activity beginning the following season. Nevertheless, we found considerable uniformity in timing of certain events, both among the three years and among individuals within the population. The integration of events in the cycle and the uniformity in timing appear to require a high degree of proximate control over the various phases.

It is obvious that several phases of the cycle are integrated and timed through their dependence on the cycles in gonadal activity. The changes in behavior and body weight, the timing of the hatching season, and the period of development of young all are consequences of the endocrine or gametogenic functions of the gonads. Thus, control of gonadal cycles is of central importance.

Lewin (1963:256) believed that the uniformity in timing of the testis cycle in California Quail and its independence of variation in temperature and rainfall indicated photoperiodic control. The same reasoning would apply to the results of this study for proximate control of recrudescence in both sexes. The abundant evidence of photoperiodic control of this phase in the cycle in various temperate-zone species generally (Miller, 1960; Marshall, 1961; Farner, 1964) and in quails specifically (Kirkpatrick, 1955; Tanaka *et al.*, 1965) supports this hypothesis.

Hungerford (1964) found indications of an influence of winter-spring rainfall and consequent growth of annual plants on the time of onset of breeding in Gambel Quail in southern Arizona. Earliest dates of calling by cocks and earliest sightings of broods were later in dry years. Lack of such a responsiveness to weather patterns in the quail of our study is probably explained by the fact that flow in the Rio Grande and in irrigation systems provides both free water for consumption and soil moisture for growth of plants. The quail in this part of the Rio Grande Valley are thus insulated by dependable sources of water from the effects of an arid climate, harsher

than that of southern Arizona. It would appear that this availability of moisture is a permissive factor allowing unmodified control by photoperiod, at least in the years of our study.

The variability in the time of gonadal regression implies a control that is less precise or less uniform than that acting on recrudescence. The annual duration of gametogenesis may be limited ultimately by the development of photorefractoriness in late summer (for review see Farner, 1964), although the lack of experimental evidence on this subject in New World quails makes this only a speculation. Nevertheless, within the potential span delimited by general photoperiodic controls, the time at which reproduction stops may be affected by a variety of social interactions and local stimuli (see Lehrman, 1959, 1964; Phillips and van Tienhoven, 1962; Brockway, 1964). We have observed, for instance, that the onset of testicular regression especially in solitary calling males but also in paired males without evident broods was later than that in the general population.

Control of behavioral changes and of the cycle in body weight has been discussed in the sections dealing with these phases. The general correlation between cessation of breeding and initiation of molt was described in the section on molts, as was the absence of a close correlation between the two phenomena in the individual bird. Causation in this phase of the cycle remains obscure. Preliminary analysis of the cycle of thyroid histology—to be reported in detail in a subsequent paper—failed to clarify the mechanisms.

Comparative and adaptive aspects. One of the most fruitful approaches to the study of adaptation has been the comparison of different groups of animals. The rationale for this approach is that correlations between differences and similarities in anatomy, physiology, and behavior on the one hand and differences and similarities in environments or niches on the other hand yield meaningful deductions concerning the origin and significance of differences and, to a lesser extent, of similarities. It is this approach that we will follow in an attempt to discover adaptational significance in the annual cycle of Gambel Quail. We will particularly emphasize certain adaptive features of the timing—in other words, ultimate control factors in the sense of Baker (1938).

Repeatedly in the foregoing accounts of the different aspects of the cycle in these Gambel Quail comparison has been made with corresponding phenomena in the well-studied California Quail near Berkeley. In nearly all features except the date of vernal recrudescence in testes in males and the length of the breeding season, the cycles in these two groups of quail were almost identical. If the hypothesis of photoperiodic control of vernal recrudescence is accepted, the difference in date of its onset in males in the two groups is readily accounted for by the difference in latitude between the two areas; that is, males of both species begin recrudescence in periods of similar daylength. Although females of the two species differ little in the timing of recrudescence, they also begin at periods of similar daylength, which occur on similar dates at the time of female recrudescence, later in the season than for males.

Although the two species are closely related and have generally similar habits, the particular populations under comparison live under quite different environmental conditions, one in an interior valley in a desert region with a short, variable, summer rainy season and the other in coastal foothill chaparral with wet winters and cool, dry summers. In view of these differences the numerous temporal similarities in their cycles are surprising, especially in the light of the striking, genetically controlled variation within such taxa as *Zonotrichia* and *Amphispiza bilineata* (Miller, 1960).

However, that timing of breeding seasons of birds is adaptive is attested by abundant evidence (Miller, 1960; Marshall, 1961), and the present example does not represent an exception. Although winters in both coastal central California and southern New Mexico are relatively mild, in both areas minimum temperatures are probably sufficiently low to prevent successful breeding much earlier than April. That these temperatures are largely a function of latitude in one case and altitude in the other and that the two regions differ greatly in total precipitation, in seasonal distribution of precipitation, and in summer temperatures are apparently irrelevant to the timing of initiation of breeding activity. Reliance upon similar photoperiods as the proximate control factor is probably in response to selection by similar winter-spring temperature regimes.

It is in the extension of breeding activity into the late summer and the correspondingly longer season that the Gambel Quail differ most obviously from their congeners in California. In California Quail of central California gonadal activity in both sexes and hatching terminate as much as a month earlier than they did in the Gambel Quail (Genelly, 1955; Raitt, 1960; Lewin, 1963). This difference appears to have its adaptive basis in the different seasons of rainfall. In southern New Mexico the principal season of rainfall is middle and late summer. This moisture and the favorable temperatures of late summer and early autumn result in favorable growing conditions for cultivated crops and, especially, for the numerous annual forbs and their associated insect fauna, which together provide the bulk of food for quail of all ages during the breeding season. In contrast, in central California, the soil moisture provided by winter rains is usually depleted before the end of the dry summer, and late summer and early autumn are not periods of active plant productivity. It is probable that the favorable late season in southern New Mexico permits extension of quail breeding beyond the period when seasonal drought prohibits successful breeding in California Quail.

Studies of the Scaled Quail (*Callipepla squamata*) in western Texas (Wallmo, 1956) and in western Oklahoma (Schemnitz, 1961) provide data sufficient for comparison of timing of breeding seasons. Wallmo (1956:83) reports hatching from early May to late August, a span very similar to those in this study. He also gives data on a small series of gonads which indicate vernal recrudescence slightly later than we found, but the timing of regression is apparently quite similar. Schemnitz (1961:34) describes a comparable hatching season but cites reports of exceptionally late breeding by Scaled Quail. This species is also closely related to *Lophortyx gambelii* and has generally similar habits and habitats, and in western Texas and western Oklahoma it lives under a climatic regime similar to that of southern New Mexico. Thus, it is not remarkable that its reproductive cycles are similar to what we have found, but the similarities do serve to confirm the similar effects of climate and general phenology upon cycles of different species.

Reproductive cycles in two more distantly related galliforms, Chukars and Ring-necked Pheasants, have also been studied in some detail (Hiatt and Fisher, 1947; Mackie and Buechner, 1963). Their cycles are, in general outlines, similar to those of Gambel Quail, but some differences in timing are apparent. The shorter period of active testes in Chukars and longer period in pheasants have been mentioned. Vernal recrudescence of testes in both groups is little, if any, later than in the quail of this study in spite of marked latitudinal difference (both species were studied at localities approximately 14° north of Las Cruces, New Mexico). Although the pheasant males were apparently active for a longer season than these quail, the data of Hiatt and

Fisher (1947: fig. 3) indicate a cessation of laying in July. In the Chukar, laying and hatching ceased earlier in the summer than in the quail of this study (Mackie and Buechner, 1963: fig. 8). Thus, these species had somewhat shorter breeding seasons, comparable in timing to those of the California Quail near Berkeley. The difference in phase relationships between vernal recrudescence and annual photocycle can probably be ascribed to the more rapid seasonal change of daylength at higher latitudes and to the necessity for temperate-zone galliforms to begin in late winter the rather long process of behavioral and physiological preparation for breeding; an early start is necessary if the first young are to be produced at the beginning of the favorable period in late April or May. The relatively early cessation of breeding in these northern populations is probably an adaptation to avoid the production of young that might fall victim to low temperatures in early autumn, a danger that southwestern quail do not face.

The general conclusions to be drawn from these comparisons are that the differences in timing of reproductive cycles in these various gallinaceous birds and, indeed, the timing in any one species—in period of recrudescence, length of season, and dates of cessation of activity—are explicable in terms of adaptation to local climatic patterns and general phenology.

SUMMARY

The annual cycles in gonadal activity, behavior, body weight, and molts in the Gambel Quail of the Rio Grande Valley of southern New Mexico were studied from March 1959 through October 1961.

Recrudescence of testes began in early February and was completed in April. Timing was uniform from year to year and synchronous within the populations. Increase in size and activity of ovaries and oviducts began about two weeks later than in testes; laying began in mid-April. As in males no annual differences were noted, and, except for a slight lag among immatures, females were well synchronized.

In both sexes gonadal regression began in June, but time of onset of regression was strikingly variable. Laying females were found as late as early August, and males with active testes throughout July. Laying persisted later in 1960 than in 1959 and 1961.

Hatching dates were computed by aging of juveniles captured later in the season. The length of the hatching periods was approximately 100 days. Terminal dates were more variable than first dates, and the period was longest in 1960 when late hatches occurred in early September.

Changes in social organization—from coveys to pairs and lone males, to families, and back to coveys—were concurrent with, and probably largely controlled by, the reproductive cycles. Various aspects of behavior involved in these changes are described. Generally, they resembled those reported for California Quail.

Body weights also followed cycles apparently influenced by reproductive status. Males were heavier than females in the nonbreeding season, but laying females were heavier than males.

Adults underwent a single, postnuptial molt, which occupied approximately 21 weeks in the individual. Onset of molting coincided with gonadal regression on a population basis, but the lack of close correlation between the two in a number of individuals argues against direct causation. Postjuvenile molting closely resembled published descriptions for California Quail in sequences within and among tracts and in correlation between molt stage and age, but it required a longer period on a population basis, presumably because of the protracted hatching season.

Integration of the various events in the cycle is largely accomplished through the dependence of many of them on the gonadal cycles. The temporal uniformity in onset of recrudescence suggests photoperiodic control. Apparent independence from effects of weather is probably due to abundant and dependable moisture from the Rio Grande and irrigation.

The cycle in these quail was very similar to that of California Quail in numerous respects; differences in timing appear to have been adaptive. The longer breeding season, resulting mainly from later extension of activity into the summer, was probably permitted by favorable temperature and moisture and consequent food. Differences in timing between these quail and Chukars in Washington and Ring-necked Pheasants in Montana and similarities to Scaled Quail in western Texas and western Oklahoma also reflect adaptation to climatic regimes.

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LITERATURE CITED

- BAKER, J. R. 1938. The evolution of breeding seasons. *In* Evolution: Essays on aspects of evolutionary biology, ed. G. R. de Beer. Oxford Univ. Press, London, pp. 161-177.
- BROCKWAY, B. F. 1964. Social influences on reproductive physiology and ethology of Budgerigars (*Melopsittacus undulatus*). *Animal Behaviour*, 12:493-501.
- DIXON, K. L. 1962. Notes on the molt schedule of the Plain Titmouse. *Condor*, 64:134-139.
- EMLEN, J. T., JR. 1939. Seasonal movements of a low-density valley quail population. *J. Wildl. Mgmt.*, 3:118-130.
- FARNER, D. S. 1964. The photoperiodic control of reproductive cycles in birds. *Amer. Scientist*, 52:137-156.
- GENELLY, R. E. 1955. Annual cycle in a population of California Quail. *Condor*, 57:263-285.
- GORSUCH, D. M. 1934. Life history of the Gambel Quail in Arizona. *Univ. Arizona Bull., Biol. Sci. Bull. No. 2*:1-89.
- GULLION, G. W. 1956a. Let's go desert quail hunting. *Nevada Fish and Game Comm., Biol. Bull. No. 2*:1-76.
- GULLION, G. W. 1956b. Evidence of double-brooding in Gambel Quail. *Condor*, 58:232-234.
- GULLION, G. W. 1960. The ecology of Gambel's Quail in Nevada and the arid southwest. *Ecology*, 41:518-536.
- GULLION, G. W., and A. M. GULLION. 1961. Weight variations of captive Gambel Quail in the breeding season. *Condor*, 63:95-97.
- HIATT, R. W., and H. I. FISHER. 1947. The reproductive cycle of Ring-necked Pheasants in Montana. *Auk*, 64:528-548.
- HUNGERFORD, C. R. 1962. Adaptations shown in selection of food by Gambel Quail. *Condor*, 64:213-219.
- HUNGERFORD, C. R. 1964. Vitamin A and productivity in Gambel's Quail. *J. Wildl. Mgmt.*, 28:141-147.

- KABAT, C., D. R. THOMPSON, and F. M. KOZLIK. 1950. Pheasant weights and wing molt in relation to reproduction with survival implications. Wisc. Cons. Dept., Madison, Wisc., Tech. Wildl. Bull. No. 2:1-26.
- KIRKPATRICK, C. M. 1955. Factors in photoperiodism of Bobwhite quail. *Physiol. Zoöl.*, 28: 255-264.
- LEHRMAN, D. S. 1959. Hormonal responses to external stimuli in birds. *Ibis*, 101:478-496.
- LEHRMAN, D. S. 1964. Control of behavior cycles in reproduction. *In Social Behavior and Organization among Vertebrates*, ed. W. Etkin. Univ. Chicago Press, pp. 143-166.
- LEOPOLD, A. S. 1959. *Wildlife of Mexico. The game birds and mammals.* Univ. California Press, Berkeley.
- 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.*, 27:346-360.
- MARSHALL, A. J. 1961. Breeding seasons and migration. *In Biology and Comparative Physiology of Birds*, ed. A. J. Marshall. Vol. 2. Academic Press, New York, pp. 307-339.
- MARSHALL, A. J., and C. J. F. COOMBS. 1957. The interaction of environmental, internal and behavioural factors in the Rook, *Corvus f. frugilegus* Linnaeus. *Proc. Zool. Soc. London*, 128:545-589.
- MILLER, A. H. 1960. Adaptation of breeding schedule to latitude. *Proc. XIIth Intern. Ornith. Congr.*, pp. 513-522.
- MILLER, A. H., and R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. Univ. California Press, Berkeley.
- PHILLIPS, R. E., and A. VAN TIENHOVEN. 1962. Some physiological correlates of Pintail reproductive behavior. *Condor*, 64:291-299.
- PITELKA, F. A. 1958. Timing of molt in Steller Jays of the Queen Charlotte Islands, British Columbia. *Condor*, 60:38-49.
- RAITT, R. J. 1960. Breeding behavior in a population of California Quail. *Condor*, 62:284-292.
- RAITT, R. J. 1961. Plumage development and molts of California Quail. *Condor*, 63:294-303.
- SCHEMNITZ, S. D. 1961. Ecology of the Scaled Quail in the Oklahoma panhandle. *Wildl. Monogr.* No. 8:1-47.
- SOWLS, L. K. 1960. Results of a banding study of Gambel's Quail in southern Arizona. *J. Wildl. Mgmt.*, 24:185-190.
- 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 conservation and management. *Calif. Fish and Game*, 21:165-256, 277-342.
- TANAKA, K., F. B. MATHER, W. O. WILSON, and L. Z. MCFARLAND. 1965. Effect of photoperiods on early growth of gonads and on potency of gonadotropins in the anterior pituitary in Coturnix. *Poultry Sci.*, 44:662-665.
- WALLMO, O. C. 1956. *Ecology of Scaled Quail in West Texas.* Texas Game and Fish Comm., Austin.

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