ANNUAL CYCLE IN A POPULATION OF CALIFORNIA QUAIL

By RICHARD E. GENELLY

This report presents an analysis of the life cycle of the California Quail (*Lophortyx californica*) based primarily on three years of trapping and observation on San Pablo Ridge, Contra Costa County, California, between 1950 and 1953. Additional observations of penned quail were made on the Davis campus of the University of California during the spring and summer of 1954. The primary purpose of my study has been to determine the extent and causes of changes in the density of California Quail on a relatively undisturbed area. Much is known of the responses of quail populations, in general, to changes in composition and distribution of vegetation, to the availability of water, and to extreme weather conditions. Yet to be explained, however, are population fluctuations of considerable magnitude, such as those noted by Emlen (1940), that cannot be correlated with obvious environmental changes. The present contribution on the annual cycle may be considered only to lay the foundation in this long-term investigation. Yearly shifts in the timing of the events of the reproductive cycle, in particular, are promising in that they suggest the importance of weather conditions to reproductive success. The fragmentary nature of my observations, while limiting their value for yearly comparisons, suggests the normal sequence and timing of behavioral and physiological events in the quail in this region.

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THE STUDY AREA

The principal area for population study (area A) was 100 acres in size, centering on the eastern slope of San Pablo Ridge, Contra Costa County, one-half mile north of Inspiration Point and an equal distance to the west of San Pablo Reservoir (see fig. 1). A contiguous area (area B) of irregular shape, lying on the west-facing slope of the ridge in Tilden Regional Park, was where most observations of behavior were made.

Area A is a small fraction of the watershed lands owned and managed by the East Bay Municipal Utility District in the vicinity. Acquisition of the land by the utility district has resulted in the elimination of most human disturbance (no public access is permitted), but grazing by cattle continues. At the present time the grazing lease limits the level of stocking to one animal per ten acres, for an eight month season, from November to June. Grazing, in other words, is moderate.

Area B is transected by a one-mile strip of winding dirt road, the "fireroad" which extends from Inspiration Point in a northerly direction along the eastern boundary of Tilden Park. This land was set aside for recreational use in 1934 and has not been used by livestock for 20 years. Use of the fireroad is restricted to emergency vehicles and to foot travel.

The topography of both areas is moderately rugged. Area A is broken up by two parallel ridges and their associated draws that extend from the main ridge down in a southeasterly direction to the San Pablo Reservoir. The area is thus composed of a series of north- and south-facing slopes. The northern end of area B is essentially similar in topography to area A. The southern two-thirds, however, is principally composed of the tops of the rounded knolls and steep slopes of San Pablo Ridge.

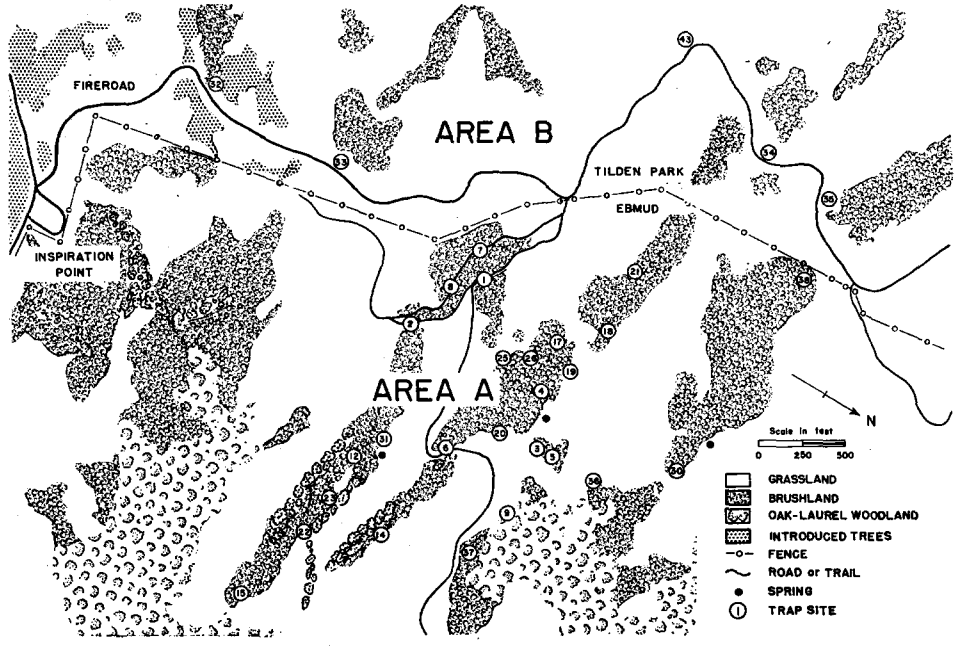


Fig. 1. The study area. The fine line separating Area A from Area B marks the crest of San Pablo Ridge.

The climate of the study area is mild. While rain falls frequently in the winter and spring months, it is practically absent in the summer and early fall. Frosts occur every year but are infrequent, whereas snow in measurable amounts may not fall for a period of several years. Ocean fogs may occur in any month of the year in the San Francisco Bay Region, and they frequently spill over San Pablo Ridge in the summer months.

The vegetation of both areas reflects the topography and land-use of each. The north-facing slopes of both areas are dominated by coyote brush (*Baccharis pilularis*) and poison oak (*Rhus diversiloba*). These species are replaced by live oak (*Quercus agrifolia*) and California laurel (*Umbellularia californica*) in the deeper canyons, well below the crest of the main ridge. A small plantation of Monterey pine (*Pinus radiata*) at the southern edge of area B is of considerable importance to the quail in that area as roosting and escape cover. Both areas are also characterized by extensive grassy slopes. These differ in density as a result of the differences in land-use. Due to the grazing of livestock, area A contains a higher percentage of forbs such as burclover (*Medicago hispida*) and filaree (*Erodium* sp.). The principal grasses are annuals dominated by wild oat (*Avena fatua*). Area B supports a much more rank growth of grasses and forbs in the growing season than does area A.

METHODS

Trapping.—The traps used went through evolutionary changes to adapt to several requirements. The material used was a galvanized poultry netting of one-inch mesh. The size of this mesh made it impossible to capture quail younger than about three to four weeks. In the first traps, a section of the netting was folded into the shape of an elongate box, 10 to 12 feet long, the edges being secured to the ground with large spikes. A small entrance funnel, made of the same material, was placed under the edge of the trap at ground level. Brush cuttings were thrown over the top to screen the captured birds from the vision of passing accipitrine hawks. A standard quail trap (Stoddard, 1931), made of ½-inch hardware cloth folded over a wooden frame and painted a dark green, seemed to be avoided by the quail. Subsequent traps were made smaller than the original model so that they could be folded up quickly and carried in an automobile. The dangle wires that were later used in the entry funnels proved necessary to forestall the exit of the few quail that became familiar with the funnel system. During the breeding season the trap could be converted to a cock-and-hen trap by placing a small cubicle of hardware cloth containing a live female within the larger trap.

Due to limitations of time and equipment, traps could not be placed at random. Since it seemed important to capture and mark as high a percentage of the population as possible, traps were placed at sites that offered the most promise of catching birds. Trapping was necessarily irregular during the three-year period, but an effort was made to devote at least a few days in each month to observation and trapping.

The most successful bait mixture contained a high proportion of small seeds, such as those of rape and millet. The quail seemed to take these small seeds at any season of the year, regardless of the natural food supply available to them or of previous familiarity with the bait. Mixtures containing larger seeds, such as wheat, barley and cracked corn were usually rejected entirely or the smaller seeds were selected while the larger seeds were left lying on the ground. Sumner (1935:190) noted that captive quail at first had difficulty in swallowing large unfamiliar barley seeds. Over a period of several days, however, the quail learned to cope with them successfully.

Marking.—Buss (1946:132) concluded from an extensive banding study of pheasants in Wisconsin, that " . . . good aluminum leg bands are not lost, but weak or thin aluminum bands may be lost in considerable numbers." Studies of various marking devices on penned pheasants at the Yountville State Game Farm (Ken Doty, personal communication) have shown that, on occasion, even "good" bands may be lost. This loss, however, is negligible since, during the course of my study of more than 400 individual quail marked in two ways (neck tags plus leg band), there was no evidence of the loss of a leg band. The bands used were supplied by the California Department of Fish and Game.

For purposes of field recognition of individual quail, a plastic neck tag such as used by Taber (1949) on pheasants was adopted. Since the tags are pinned to the bird through the loose skin at the back of the neck, they are apt to be torn out if they happen to catch in the vegetation. This would be more likely to happen in quail than in pheasants, since the former generally inhabit thicker brush cover. In spite of this objection, a modification of the "Taber tag" proved successful.

These tags were made of a common plastic upholstery material that is available in a variety of colors. They were secured to the bird with a short length of stainless steel wire. The wire was first passed through the eyelet of one tag, then spiralled tightly back upon itself and the short end clipped off. The other end was pushed through a fold of loose skin at the upper side of the base of the neck so that it emerged on the far side of

the spinal feather tract, where it was attached to the other tag. Tags of plastic .02 inches thick and cut to ½ inch by 2¼ inches in size were found to be most efficient. Thinner material became brittle within a few months and cracked off near the base, whereas larger or heavier tags seemed to burden the bird unnecessarily. Tags of this size, if tightly secured through the skin, permitting no more than ½ inch of wire between the bases of the tags, will be exposed about one inch beyond the tips of the contour feathers, thus providing sufficient exposure for an identifying symbol. Single letters or numbers were cut from the same plastic material of a contrasting color and were fused to the tag by heating with an ordinary electric iron. This process turned out to be the weak point of the marking system, since the success or failure of the fusion process could only be established after several weeks. In several instances symbols were fragmented or lost altogether. The success of marking for individual recognition, then was variable. But when a symbol was intact, the identification of individuals appeared to be accurate. Even fragmented symbols were sufficient for recognition in most instances.

Age determination.—Criteria for segregating young from adult California Quail were reported by Sumner (1935). Throughout the first year of life, the presence of juvenal greater upper primary coverts, which are mottled rather than uniform in color, is the best indication of a first-year bird. For a few weeks after these coverts have been dropped, however, young birds may still be recognized, although with less reliability, by the presence of the more pointed distal primaries—the last juvenal feathers to be molted. Thus, it was possible to classify all adult-appearing birds into two age groups: those hatched in a given year and those hatched in prior years.

Young birds in their first summer could be aged much more accurately. Petrides and Nestler (1943) used the rate of replacement of the primary remiges during the postjuvenal molt of the Bobwhite (*Colinus virginianus*) as a basis for age determination. More recently, Petrides and Nestler (1952) estimated the error of dating by this method to be plus or minus one week until the tenth week of age. Thereafter, the accuracy of the method declined rapidly with the increased variability in the rate of replacement and of feather growth.

The data obtained on the postjuvenal molt of wild California Quail on San Pablo Ridge, together with molt data from captive quail, show that the rates of replacement are close to those described for Bobwhites. This method was used to establish the hatching dates of young quail captured in the summer and early fall months.

Observation and census.—In addition to the opportunity for observation afforded by trapping activity, blinds were set up adjacent to "cock and hen" traps in the spring months to facilitate close study of behavior. Ordinarily, however, traps were watched with binoculars from distances which made careful concealment unnecessary. In the final year of the study, an automobile made an excellent blind from which to watch the quail along the fireroad in Tilden Park (area B). The most intensive and satisfactory studies of marked quail were made in this manner. The area was visited whether for trapping, observation or censusing, on 330 days in all. An annual census was taken in November or early December of the years from 1951 to 1953. Each census was accomplished by three or four men accompanied by dogs. The quail in area A alone were counted as they were flushed up over the drivers. The counts thus secured agreed reasonably well with the calculations of abundance derived from trapping returns for the corresponding periods.

PAIRING

Courtship behavior.—Little has been published on the courtship behavior of California Quail. In spite of an elaborate enclosure set up by Sumner (1935) to study be-

havior, the secretiveness of the birds at this season made observation difficult for him. Stoddard (1931:17), however, was able to observe pairing in Bobwhites under pen conditions. Pair formation was preceded by a frontal display by the males in which "The head is lowered and frequently turned sideways to show the snowy-white head markings to the best advantage, the wings are extended until the primary tips touch the ground, while the elbows are elevated over the back and thrown forward, forming a vertical feathered wall. The bird . . . puffed out to the utmost . . . now walks or advances in short rushes toward the hen." At first, the hens appeared to pay little attention to the males, but "in two cases the first evidence noted of selection was when the hen suddenly squatted and gave a scarcely audible note, and copulation took place. This was repeated frequently, and the pair appeared inseparable thereafter."

In the California Quail, pairing appears to occur primarily within the covey, but no observations of males displaying before females in the manner described by Stoddard were made under conditions that were entirely "natural." Female quail were used as trap decoys for unmated males during the breeding seasons. In almost every instance when the males approached a trap containing such a female, they would display before her, even though briefly, in the following manner: The body feathers would be fluffed out and a low series of "conversational" notes begun. Next, the head would be lowered and extended straight forward and the wings extended from the body an inch or two and drooped until the outer primaries touched the ground. The tail would be elevated to an angle of 45 degrees above the horizontal and the feathers spread out. The subsequent forward rush of the unmated male against the wire of the trap implied a similarity of function to the "rush" in Bobwhites.

The factors which enter into the selection of a mate by quail are difficult to analyze. Observations of penned quail, however, suggest that there may be individual recognition at an early stage of "acquaintanceship." During the spring of 1954, a small group of captive California Quail, brought in from Napa County, were kept in a 20×20 foot pen on the Davis campus of the University of California. This pen was located in the range of a wild population of quail. Among the captives the sex ratio was 6♂♂:13♀♀. From February 23 on through mid-summer, "lonesome" unconfined males were almost constantly seen closeby or atop the quail pen. These males seemed to appear one at a time and take up residence along the side wire of the pen that was closest to the quail roost on the inside. Within a few days the newest arrival would be trapped and released within the pen, whereupon another wild quail would assume the position on the outside of the pen. On March 3, 1954, when the second unmated male took up "residence" beside the pen, it was noticed that a particular female seemed to be responding to the outside male. When he sat on a twig that protruded through the side of the pen, she, too, would perch on the same twig with only the wire netting separating them. When he would drop to the ground from her sight behind the baseboard, she would run back and forth along the inside of the same baseboard, apparently seeking a way to join him. Later the same day, the 19 quail within the pen were marked to facilitate recognition of individuals. On the following morning, the same behavior between the "pair" was seen and, at that time, the female was noted as being yearling number 6710. In the afternoon, the yearling male entered a trap in the baseboard of the pen, was banded number 6727, tagged for easy recognition, and released within the pen. At the next opportunity for observation on March 6, male number 6727 was seen feeding within the pen in close company with female number 6710 and attempting to copulate with her. There seems to be little doubt that the initial phases of pairing in this instance had occurred through the intervening wire netting and that these birds were able to recognize each other despite the shortness of the period of acquaintance.

Stoddard (1931:18) noticed similar behavior among his penned Bobwhites. At the time of pairing "It was noticeable that certain cocks were especially attracted by certain of the hens almost from the first, and even though not necessarily the most successful in combat, they were more persistent in their attentions than the others."

Relationship of prior mating to pairing.—Of the 29 pairs for which there are reasonably complete data, only one pair appeared to remate in two consecutive years. However, only five of these 58 quail were observed for more than one sason; mortality and movement combined to eliminate the majority from further observation.

Adult female number 214 and yearling male number 215 were first captured on August 26, 1951, in trap 7, at which time they appeared to be a mated pair. Subsequently, they were captured together on January 27, 1952, in trap 26, on February 17 in trap 25, and on April 28 in trap 21, at which time female 214 appeared to be laying.

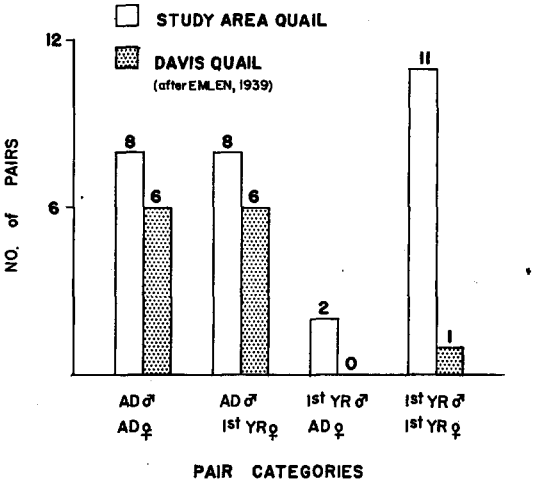


Fig. 2. The relationship of age to pair formation in two populations of quail.

The male was last seen in company with his mate near trap 19 on July 2, 1952. The female was again captured with some old covey mates at trap 2 in mid-September.

On the other hand, there is good evidence that many quail change mates between breeding seasons even though they are closely associated with their mate of the prior season all through the winter period.

Relationship of age to pairing.—An examination of the age class of the members of 29 marked pairs furnishes some interesting clues for speculation on social behavior. In figure 2, the frequency of matings of quail of two age classes, adult and first-year, are shown. The data indicate the infrequency of matings between first-year males and adult females. Indeed, one of two such records is open to some doubt since one pair was not recorded until August 26, at a time of year when the pair bond is difficult to detect. It seems probable that the pairing of first-year males with adult females occurs late in the breeding season in the event of some mishap to the original mate. Pairing prior to covey breakup principally involves the older birds, the younger quail apparently being forced to seek mates elsewhere. Probably this situation is due to an earlier physiological "awakening" of the adult males, such as that encountered in the earlier laying of the older females, which gives them the "jump" on the first-year birds. Matings of adult

males to adult females occurred with the same frequency as that of old males to first-year females. Ostensibly the latter category is a result of the imbalance in sex ratio of the older birds. Emlen's data (fig. 2) for pairs of first-year quail may have been incomplete, since he knew the age of pairs that were seen in the first half of the nesting season but lacked age data for late-season pairs. Pairs composed of first-year birds occurred frequently on San Pablo Ridge. Other factors which combine to produce the sex and age ratios in the population could doubtless profoundly affect the pairing ratios here indicated.

The pair bond.—Pairing normally begins in late February or early March. By the middle of August, the formation of the coveys is well along. By this time also, most of the unmated males have ceased crowing and joined the local group of unsuccessful adults or a family group. Pairs with broods are still held together by their attentions to the young but in adult groups the sexes once again freely mingle during feeding. Fighting between the males is no longer associated with a quick return to the side of a female. Pairs have been combined into groups.

The attachment of the members of a pair for one another increases to a peak in April and May, but dwindles during the summer months. During the early weeks of the breeding season, the attachment of the members of a pair for each other has not yet reached a point where the paired birds remain close together during most of the day. Thus on April 7, 1951, 12 quail, six males and six females, were seen foraging near trap 1. Although the birds were marked and known to be paired, they intermingled freely and without friction. However, only three days later, on April 10, the same birds behaved quite differently. Now the members of the different pairs did not intermingle but were well separated during foraging, and frequent skirmishes were seen between the males. It was evident that part of this behavior was initiated by the presence of at least two unmated males that had joined the group.

By mid-June the members of a pair were very seldom seen to wander more than five or six feet apart during feeding. Practically no intermingling occurred at this season which did not result in skirmishing or fighting between the cocks. The increase in the degree of association between the members of a pair was closely paralleled by the increase in the aggressiveness of the unmated males in the vicinity. Hence the strong pair bond in California Quail may be, in part, a result of the distorted sex ratio which always leaves some males without mates.

CALLING

The principal objective in studying the calls of quail was to seek "indicators" of seasonal behavioral changes. The calls and notes of California Quail are numerous and diverse and have many important functions in the lives of these birds. Sumner (1935: 200-205) has described many of them in detail.

The most familiar call is the "assembly" call. While it is known to be given by both male and female quail during all months of the year, there is a marked seasonality in the intensity of calling correlated with events in the annual cycle. The most intensive calling was found to occur in the fall months during covey formation. Calling declined during the winter, but increased in early spring during pair formation and covey breakup. The use of this call in May and June was principally by unmated males; pairs did little calling unless male and female became separated. Least calling was heard from mid-June until mid-August.

Shortly after the beginning of pairing, each spring, the first "cow calls" were heard. This call consists of a single note that is "similar to the last note of the assembly call" (Sumner, *loc. cit.*) but is louder and usually given only by the unmated males. During

the present study, only one instance of a mated male giving the call was noted. A captive female gave the call on at least two occasions. These instances, however, are probably of infrequent occurrence. The "cow call" apparently functions as an announcement of territory, a matter that is taken up in more detail elsewhere.

The date of the inception of "cow calling" is a reference point for comparing the phenologies of breeding seasons. "Cow calls" usually began in late March, rose to a peak of intensity in May and declined rapidly in early June. First calls were heard on March 20 and 23 in 1951 and 1952, respectively. In 1953, however, the first calls were heard on March 7. This advance in the season was later matched by a similar advance in the hatching dates of young and may have borne some relationship to the success of that reproductive season.

There is little value in the use of the final date on which this call is heard in gauging the duration of the breeding season. After the noticeable decline in calling in June, occasional "cow calling" was heard until late August, but many of the intervening days passed without any calls being heard.

A special effort was made to determine, quantitatively, the date of the peak of call intensity. In general, it appeared that in early season calls were uttered by individual males at a mean rate of four per minute. This rate increased to between six and seven per minute by May, but in any one day there was considerable individual and even hourly differences in the rate of calling. Calling was increased by fair warm weather, by the presence of female quail, and by the calling of competitors. It slowed down noticeably in the absence of these conditions and in midday. In May, however, even poor weather was not sufficient to quiet unmated males entirely. All these variables made the establishment of a peak season subjective.

The "squill call" (Sumner, *op. cit.*: 203) also appeared to be given only in the breeding season. This call, however, accompanies the threatening and fighting behavior between the males. It is never uttered as a general declaration, in the manner of the "cow call," but always appears to be directed to a nearby adversary. Its frequency of utterance, therefore, reflects chance meetings and the general social unrest of the breeding season.

A third call associated with the breeding season, the "pseu" note of distress, is considered elsewhere (p. 276). Males displaying before captive females uttered low harsh "throaty" notes that seemed to be reserved for the occasion.

A variety of other calls and low notes were heard during the three seasons. The familiar series of "clicking" notes associated with warning and alarm is given with emphasis befitting the situation at all seasons of the year. Many other calls, usually referred to as conversational notes are scarcely audible at 20 feet from the bird, but appear to function in maintaining contact between individuals of the group.

FIGHTING

Quail fighting is here taken to include every act of animosity from the merest threat to a full-fledged cockfight. In the former category, quail frequently were seen to commit acts which appeared to be reminders to others of their position in the peck-order. This type of behavior, of course, was most frequently seen when the quail were feeding together in flocks in the winter. In chance encounters, one male was often seen to jostle against another or peck gently at another male that came too close to him. Usually the male that was the target of such a slight show of aggression would yield by retreating a short distance. If the aggressor became more perturbed at the presence of the intruding male, a short pursuit might develop.

Threats between males, regardless of social status, were seen to be composed of elements of the display used by the unmated males before trapped females. All elements of this display, however, were not used in threatening gestures to another male. Thus, a slightly lowered head was the beginning of a threat which was clearly "understood" by the recipient. In most instances, however, this type of threat would be followed by a short dash at the object of the threat, to lend emphasis. Drooped wings and ruffled feathers seemed to be a more advanced element of threatening, whereas the elevation and spreading of the tail came last. The erection of the feathers on the crown of the head was thought to be a part of the lowering of the head, but this could not be verified at the distances that observations were usually made. The ruffling out of body feathers, however, was commonly seen. The body, head, and wing positions assumed by the female during copulation are very similar to this. The tail position of the female, however, necessarily differs. Females were also seen to threaten in a manner similar to that of the males.

Full-scale fighting involves behavior which is similar to that seen in other gallinaceous birds. Opposing males face each other squarely and duel briefly but viciously with their beaks prior to leaping up and down in the cockfight. Excited and sharply-delivered "squill calls" quite often accompany the fighting and are invariably given at the completion of the fight. Leaping apparently is an end result of sparring with the beaks to seek an advantage over the adversary. Similar leaping by pheasants and domestic fowls while engaged in fighting is also to gain advantage but more importantly is necessary in bringing the spurs into position for effective use. In the quail, the feet are not used as a weapon, the beak being the sole weapon of offense. It is most often aimed at the nape of the neck of the opponent, where it may do considerable damage if fighting continues for any length of time. The wings may also be active during a pitched battle, but these seem to serve the quail in maintaining balance rather than as a weapon.

Most fights under natural conditions lasted little more than a few seconds and hence had no observable effects on the combatants other than to dislodge a few feathers. Under artificial conditions, as in traps, however, when the "loser" is unable to evade his pursuer, serious injury or death may result. Such an instance was recorded on May 13, 1953, when adult male number 746 was found badly beaten in trap 35 with first-year male number 570. The inside of the trap contained many loose feathers and the back of the adult's head was devoid of feathers. The skin of the nape region had been punctured and was severely inflamed. Stoddard (1931:17) recorded similar instances among Bobwhites in which males trapped in April would be found with "the neck vertebrae . . . picked bare by the victorious cock."

In figure 3, the intensity of fighting is based on two elements. The proportion of the population which is involved in the fighting forms one element. The second element involves the degree of contact between fighting individuals. In general, it appears that the greater the proportion of the individuals that were involved, the greater was the degree of contact in individual encounters.

Defense of mate.—As brought out earlier, most of the fighting that occurred in the quail population from March through June was directly related to pair bond maintenance. Furthermore, it seemed that the great majority of these fights were between mated males and unmated males. The increasing intensity of these fights until the end of May was related to the increase in the aggressiveness of both the unmated and mated males. The interest of the unmated males in pairs, or, at least in the females, was noted by Emlen (1939:126). The result of this interest was a close association of unmated males with pairs during the periods of feeding. This close association repeatedly led to the fighting off of the unmated males by the mated males.

While most of the fighting was confined to the males, females occasionally showed their interest in maintaining the pair relationship intact. On April 10, 1951, near trap 1, a female of a pair that was feeding near a lone male suddenly lowered her head in a threatening manner and dashed at the male. As the latter gave ground rapidly, the female when five or six feet distant from her mate, gave up the chase and returned to his side. A few moments later, the hens of two unmarked pairs that had chanced to draw together while feeding, began threatening one another. Shortly, they became involved in a leaping duel of beaks while their mates looked on. Usually, however, active fighting was restricted to the males at this season.

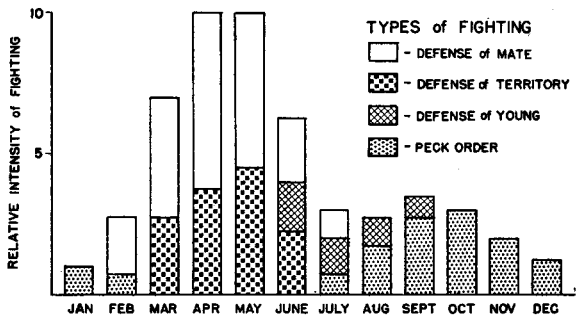


Fig. 3. Frequency distribution of fighting of quail.

The fact that California Quail coveys break up in spring and that pairs spread out over the countryside to nest suggests the possibility that the pair may actively defend the vicinity of the nest against others of their species. Such a conclusion was drawn by Schwartz and Schwartz (1949:51) for the California Quail introduced in Hawaii. "Following separation from the others, the pair spends a month or more selecting a territory, usually within the covey's range, where the female will build her nest and which her mate will defend against intruders."; in addition (p. 59), "cocks will tolerate little trespass in their nesting territories." Such was not found to be the case in the Bobwhite (Stoddard, 1931:27). When suitable nesting sites were limited, several pairs of Bobwhites would nest in a small area. Intensive studies of the nesting Bobwhites failed to reveal them committing any acts that would suggest active defense of the vicinity of the nest against other Bobwhites. Indeed, Stoddard found that two or three hens might commonly lay their eggs in the same nest.

No observations of quail behavior at the nest site were made during the present study, but the available evidence suggests that California Quail, as well as the Bobwhite, do not actively defend a nesting site. Moreover, the females, like the female Bobwhites, are strongly suspected of contributing their eggs, at times, to a common nest (Tyler, 1913:34) and are known to do so in captivity. At the completion of several years of careful observation on this species, Emlen (1939:126) stated: "mated pairs did not set up nesting territories in the usual sense of the term."

The unmated males.—It was Stoddard (1931:97-104) who first noted that, contrary to widespread popular belief, it was the excess males in the breeding population that were responsible for the well-known "bobwhite" call, rather than the mated males. Similarly, the single "cow call" of the California Quail, heard only during the spring and summer months, was noted by Sumner (1935:201) to be given only by unmated cocks. Emlen (1939:126) confirmed Sumner's observation but qualified it when he observed

that the mated male occasionally may give the call when his mate is out of view. Stoddard (*op. cit.*:101), again, was the first to note that "the majority of unmated cocks . . . take up 'territory' from which they whistle day after day." The fact that one of these unmated males was known to move a mile from the original point of capture in a "cock-and-hen" trap, further led him to conclude: "it seems probable that some individuals leave their 'territory' for a short time in search of mates." Emlen's study (*loc. cit.*) of California Quail verified that at least some unmated males of this species were also territorial. He found that of eight unmated males at Davis during the summer of 1937, four "lived in a nomadic existence and four others . . . were decidedly sedentary. Each bird in the latter category restricted itself to a small crowing territory near the nest of an established pair." In the present study, considerable effort was made to learn more of the territorial behavior of these unmated males, of their relationship to breeding pairs, and to the other unmated males referred to by Emlen as "nomadic."

Territoriality.—Perhaps the most obvious manifestation of territoriality by the excess males in the breeding season is the spacing of individuals giving the "cow call." From shortly after the first unmated males were heard calling in March until mid-June, it was possible on any clear day to plot the location of these males on a map. Unfortunately, due to the hilly nature of the terrain as well as to the abundance of heavy cover, it was seldom possible to identify the caller, even if he was banded and marked. Moreover, it soon became obvious that although the majority of the paired quail in the area were usually marked and identifiable, a high percentage of the calling quail were not.

The accumulation of maps shows that up to ten excess males were present and calling on area A at one time, that they were spaced at distances ranging from about twenty feet upward, and that the highest density of unmated males occurred in the area favored by the nesting pairs. Figure 4 contains all the location records of crowing males for the three breeding seasons, 1951-1953, that were plotted in the field. It shows the relative frequency with which different parts of the area were used by these males, and their relationship to the vegetation. The area of the greatest density of dots shows that most of the activity of these males was centralized in the large island of cover adjacent to trap 4, which also was the concentration area of nesting pairs. Relatively little nesting appeared to occur in the draws near traps 14 and 22. In the winter season, however, these draws are the centers of activity of two large coveys. It was also clear that, from the number of callers involved at any one time, "nomads" as well as "sedentary" unmated males were involved.

Territorial fighting between unmated males appeared to be of frequent occurrence. However, interactions of this type in which the identity and status of all of the principal participants was positively known were few. In one case, an adult unmated male (no. 773) who had moved into the vicinity of trap 33 in company with several pairs from trap 35, set up a territory around the principal feeding ground of these pairs. He successfully defended this area against the encroachments of other unattached males (including adult male 754) for more than a month, but mysteriously disappeared in late May. His territory was taken over within a few days by unmated male 754, who thereafter successfully repulsed other unmated males for the remainder of the breeding season.

Male behavior at cock-and-hen traps in the breeding season also reflected the territoriality of many of the unmated males. The usual pattern of response to a calling captive female quail was as follows: an unmated male would call from a distance in response to the female, then fly to the site of the trap. In several instances, the failure of responding males to fly closer than 50 to 100 feet to the trap suggested their concern with some threat near the trap, possibly the threat of an unmated male of superior

fighting ability. Less inhibited males, upon sighting the lone female, would run rapidly toward her. At this point, behavior varied between the assumption of a quiet alert position near the trap (15 instances) or a brief display and headlong rush against the trap wire (3 instances). In either case, there followed a period of inactivity as both captive female and frustrated male quieted down. Within a few minutes, however, this phase would usually be interrupted by the approach of a second unmated male (11 instances).

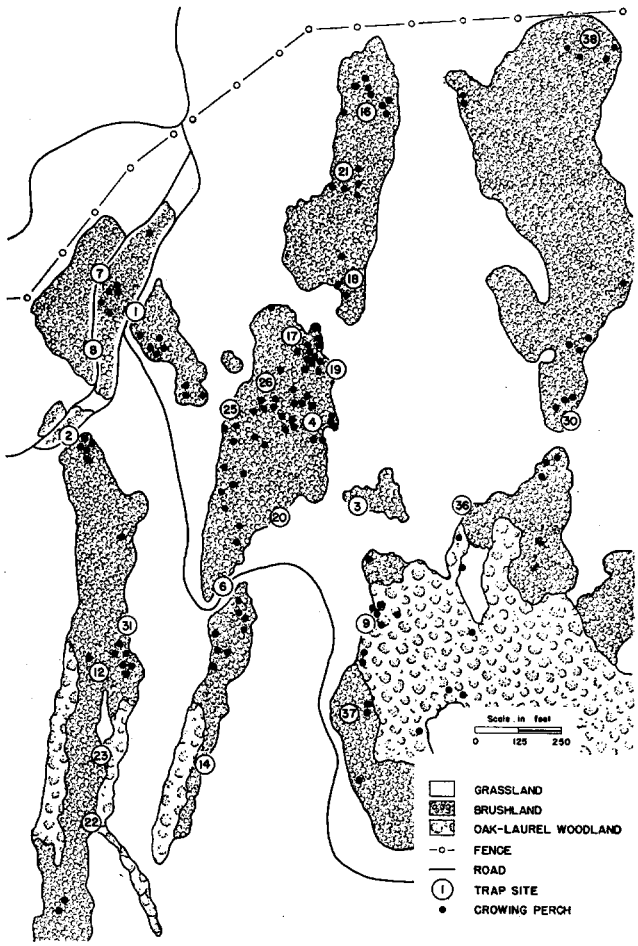


Fig. 4. Spacing of crowing cocks. Each black dot represents a site from which a male delivered the "cow call" in 1951, 1952, and 1953.

On each of these occasions, the first-arrived male would rush forward to drive the newcomer away. The fact that the outcome of these encounters did not invariably result in the successful repulsion of the second male by the first (the second male in four of eleven such encounters drove the first male off), suggested that the territory-holding male did not always reach the trap first. Hence, any slight psychological advantage the first male might have gained by the brief association with the female (mated males, regardless of size, invariably are successful in repulsing all unmated males) was insufficient to over-

come the fighting superiority of the territorial male. Moreover, the involvement of marked males in some of these encounters supports this conclusion.

On theoretical grounds one would expect that the greatest percentage of unmated males in a population would be first-year birds, since they outnumber adult males. Nevertheless, in the sample of 20 unmated males from San Pablo Ridge (fig. 5) it is seen that only eight of these were yearlings, while twelve were two years old or older, and two were three or more years of age. At Davis in the spring of 1954, another sample of 12 unmated males was taken. These birds were trapped as they appeared beside a pen containing some unmated female quail. Here the first-year males outnumbered the older males by ten to two.

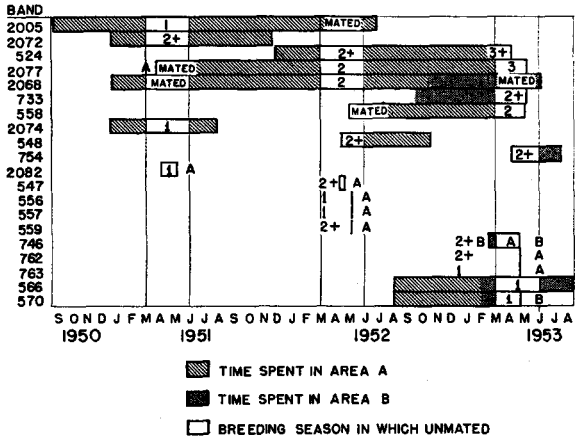


Fig. 5. A summary of the breeding status, age and movements of 20 male quail. The record only includes those males known to be unmated in one or more breeding seasons. Length of the horizontal bar represents the length of the period between first and final observations. A single short vertical line indicates a single observation. Numbers refer to age in years. Capital latters represent study area where observed or captured.

The apparent differences between the two quail populations might be accounted for by the different sampling techniques used. Most of the unmated males captured on San Pablo Ridge were attracted to a cock-and-hen trap. These traps were used at many different trap sites and hence probably in the territories of several older unmated males. Territorial males would be most apt to challenge the presence of strange quail within their area as well as to show interest in unattached females. At Davis, however, all the trapping was in a single locality, thus the trap was available to the unattached or "nomadic" unmated quail, after the removal of the territorial male. In short, the apparent differences of the frequencies of the older males of the unmated category in the two populations, are perhaps not real. The Davis population is hunted and as a result probably contains a larger proportion of young birds, but this difference of itself would not account for great disparity in ratios here obtained.

The predominance of the older males in the sample from San Pablo Ridge suggests that the older males are usually the dominant, territory-holding individuals. Conversely, the nomadic unmated males would be represented principally by yearlings, although

some subdominant adults would be expected in this category. Some support for this is found in figure 5, where it is seen that unmated yearling males, for the most part, had short observation records while the older unmated males had the longer records.

In summary, fighting which involves unmated males is principally concerned with the maintenance of crowing territories. Shortly after the beginning of the crowing season in March, the males may be seen to disperse about the area where they devote a good part of their time for the next three months to giving the "cow call" from a suitable perch. All unmated males, while they appear to be primarily concerned with keeping in close company with paired quail, especially the females, are usually intolerant of other excess males. Two classes of unmated males may be differentiated according to their ability to advertise and defend a territory near the nests or feeding grounds of one or more pairs of quail. Territorial males are usually the older birds, while the "nomadic" unmated males are principally first-year males.

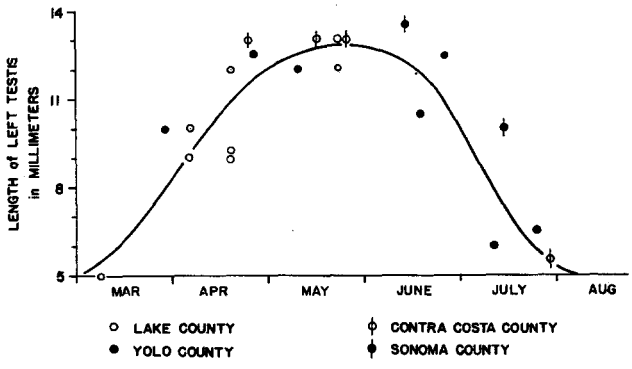
Defense of young.—The solicitousness of quail for their young is comparatively well known. Wild unmated male Bobwhites, when placed in captivity with young quail that were hatched artificially, have been found to "adopt" the young (Stoddard, *op. cit.*:65). Furthermore, parent Bobwhites will vigorously defend their young against enemies much larger than themselves (*op. cit.*:42). Strange quail that attempt to interfere with a brood may also find themselves set-upon by the parents or foster parents of that brood. Similar observations were made on California Quail.

The "pseu" note described by Sumner (1935:205), and given by both young and adults when in distress, almost invariably stimulates a response from other adult quail. In the present study captives that had been removed from traps were kept in bags nearby awaiting their turn to be weighed. In the event that a quail during handling emitted the distress call, the bagged quail would make wild efforts to escape. This behavior would ensue until discontinuance of the notes. On August 12, 1951, an adult male quail being removed from a trap for banding began to give this cry. The response from several wild quail, some distance up a hill in thick cover, was instantaneous. In contrast to Sumner's observation (*op. cit.*:205) that quail in the "free state" crouch down and remain silent when they hear the "pseu" note, these birds gave the same distress notes and moved rapidly down the hill to within eight feet of me, under cover of the brush. By imitating the note, it was possible to cause two of the males to fly up out of the cover, thus exposing themselves to unknown dangers in their excitement. The fact that both the bird that gave the first calls (D2010) and the most agitated reactor (D2087), were adult males suggests that this call is not only associated with parental defense of young but is a releaser of a type of "mobbing" behavior that would be useful in the distraction of enemies. Similar behavior was set off on subsequent occasions by whistled imitations of this note, but the response was not invariable. Moreover, the response of wild quail to the call appeared to be seasonal (fig. 3) and coincided with the period when the young were under the guardianship of the adults.

Fall and winter fighting.—Fighting between quail in fall and winter was concerned with covey formation, and apparently, with individual adjustments within the coveys. Emlen (*op. cit.*:129) noted pitched battles between the members of strange broods that chanced to meet in mid-September. Fighting that involved many quail was seen on the fireroad on October 26, 1952. At this time, the great amount of calling and the excitement of the participants suggested the meeting of two socially exclusive groups. Encounters of this intensity, however, were not observed in mid-winter.

All the fighting and threatening that occurred in the winter months was between males and may have been associated with the establishment and maintenance of social rank. Fighting between two males within a subcovey near trap 33 occurred during the

feeding period on August 2, 1953. All the other members of the group seemed to be compatible and moved along together as a single group. Later in the year in all coveys, the frequent observation of one male threatening another, together with the apparent recognition of the superiority of the aggressor by the subdominant quail, strongly indicated the existence of a dominance order among the males. The existence of such a "peck order" is well known for the domestic fowl and has been reported among females of the Ring-necked Pheasant (Collias and Taber, 1951).



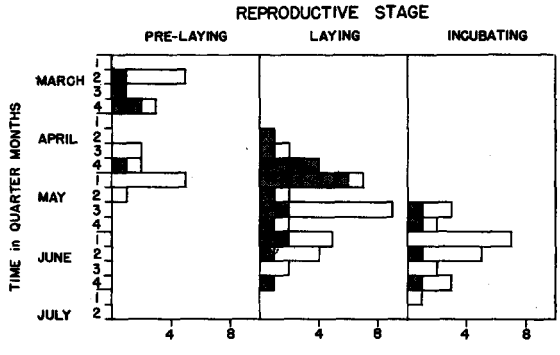


Fig. 6. Above, the testis cycle. Each symbol represents one record. Below, the female reproductive cycle. The data are from birds trapped in 1951, 1952, and 1953. Shaded bars are adults; open bars yearlings.

REPRODUCTIVE CYCLE

Male.—A crude testis cycle has been plotted (fig. 6) from material gathered from several localities during the years of the study. Insufficient data are available for a comparison of yearly phenologies. Since the collection of males from the study area for this purpose was impractical, due to the nature of the study, a few quail were collected in each of the months of the breeding season from nearby in Contra Costa County (5), as well as from Sonoma (2), Lake (8) and Yolo (7), counties, California. The latitudinal spread of this collection is slightly in excess of one degree. The resultant curve corresponds with the cycles in calling and behavior already discussed. The length of the left testis has been used as a basis for comparison as it is usually the larger of the two and

hence can be more accurately measured. Incomplete measurements for some of the specimens collected earlier made comparison of total testes volume, a more desirable datum, impossible.

It may be seen in figure 6 that winter-collected adult males had testes approximately five millimeters in length. The increase in length appears to occur in late February or early March at a time when pairing activities become noticeable. Testis size increases rapidly during March and reaches a peak by late April. The decline in size begins by mid-June, and by the first of August the organs are again back to their minimum size. The rate of decline may be slightly more rapid than that of increase. During seven months of the year, therefore, the testes are in a relatively quiescent state.

Female.—The data for figure 6 were gathered from live-trapped females principally in the breeding seasons of 1952 and 1953 in both area A and area B. Insufficient data were obtained to warrant the comparison of yearly phenologies or to justify a comparison between the females on the two study areas.

The classification of females into three categories, "pre-laying," "laying" and "incubating" is based on a combination of physical characteristics. Weight was one criterion. Hens that weighed less than 200 grams when removed from a trap in April and May usually had not yet begun to lay. The rapid increase in weight at the beginning of laying seemed to be due to two factors. First, the increase in the ovary and oviduct could account for about 16 to 20 grams of the rise in total body weight. The extreme weights of some of the hens, however, were undoubtedly due to their having gorged on the trap bait. Observations of hens at traps supports this conclusion, since they always fed rapidly and seemingly incessantly at this time. In the domestic fowl, laying condition is associated with increased size and content of the alimentary tract.

Additional criteria for classification were the condition of the cloaca, whether large and wrinkled (laying) or small and smooth (not-laying), and the distance between the tips of the public bones, which were about two centimeters apart when the hen was laying and only one centimeter prior to laying. Accompanying the spreading of the pubic bones was an increase in ovary size which was reflected in the increased distance between the posterior tip of the keel of the breast and the cloaca. Gentle palpation of the ventral abdominal region left little doubt of the hen's status if a shelled egg were present in the uterus.

Laying began by the second week in April, reached a peak by the third week in May, and declined through the month of June. During the first month following onset of laying it was notable that only two of nine first-year females had begun to lay, while nine of the eleven older females captured were laying. Lehmann (1953:222) made similar observations on the Bobwhite in Texas. In April and "prior to the May rain" in 1950 and 1951, ten of 16 old females were breeding, while only five of 37 yearling females were breeding. It appeared to Lehmann that "early breeding, . . . on dry range, is principally by older birds with young of the previous year requiring comparatively verdant conditions for general breeding." Four captive adult California Quail at Davis in 1954, that were exposed to the same conditions as six yearling females, also began to lay in advance of the younger birds. It appears, therefore, that this is generally true for two species of quail and may apply as well to other species.

The time of day at which female quail drop their eggs could not be directly determined in the field, but trapping data are suggestive (table 1).

The high percentage of egg-bearing females captured at 6:00 and 7:00 a.m. (Standard Time) indicate that the eggs are usually not dropped until at least two to three hours after the beginning of daily activity and probably not until mid-morning. At Davis, five eggs laid by three different captive females appeared in the following time

Table 1

Hour of the Day and Presence of Shelled Egg in "Laying" Females

Time of day	Female with egg in oviduct	Female without egg in oviduct
5 a.m.	1	0
6 a.m.	18	3
7 a.m.	7	1
8 a.m.	1	1
6 p.m.	1	1
7 p.m.	3	0

intervals: one each between 7:00 a.m. and 2:00 p.m., 7:00 a.m. and 11:00 a.m., and 7:00 a.m. and 10:00 a.m.; two were dropped between 7:00 a.m. and 9:30 a.m. It is quite probable, however, that a cycle in the laying of quail eggs, similar to that of the domestic hen (Hutt, 1949) exists which would mean that there would be considerable variation in the time of laying at different periods of the cycle. Stoddard (1931:26) recognized the existence of such a cycle in the laying of Bobwhites. One female Bobwhite was seen to lay at 9:40 a.m. Other hens, laying in a common nest, "came in to lay at different hours."

The laying records of individual wild California Quail indicated their persistence in renesting and raised the question of the rate at which quail lay. In 1952, adult female D2096, when captured on April 28, was classified as "laying" by her weight and by the appearance of her cloaca, although no egg could be palpated. On May 16, she was definitely laying, as she subsequently was on June 14. It is quite possible that she had ceased laying for a time between captures. On the other hand, it is not known how long she had been laying prior to the earliest date and subsequent to the June capture. In any event, her egg production was probably substantial and eventually resulted in a clutch that was successfully hatched and reared.

Since quail are indeterminate layers, removal of their eggs will result in their continued efforts to complete a clutch. The laying records of eight captive females, kept at Davis in 1954, give an impression of the potential rate of laying. The mean rate of five eggs per week for the captives was constant from the time of the first egg throughout a thirty-day period. At the end of the period, the mean number of eggs per bird was 21.5 and the extremes 16 and 26. It is quite likely, however, that wild quail, better able to select their own diet, would have a slightly higher mean rate.

The appearance of the first signs of the "incubation patch" was cause for placing the bird in the third category, even though laying was still in progress. Careful examination of live-trapped females showed that the incubation patch varied considerably between individuals but had features in common with that of passerine birds (Bailey, 1952).

The first noticeable clue to the development of this area was the loss of down feathers from the lateral ventral apteria of the breast region. Second, in most instances, defeatherization was completed by the loss of the remainder of the down from the apteria and of many of the contour feathers from the ventral tract, thus uniting the lateral and median patches. In this advanced state, the inner surfaces of the upper legs were devoid of feathers as well as the lower abdomen anterior to the cloacal region. This stage was reached, for the most part, in June, after incubation had been in progress for many days. Egg laying frequently accompanied both the early and advanced stages of defeatherization. It seemed, however, that the association of laying with the latter stage was probably coincident with renesting. Since May 27 was the earliest date at which a

fully developed incubation patch was noted, it appeared that incubation must begin prior to the completion of the defeatherization process. However, no direct evidence on this point is available. It was certain that the initial stages of development of the incubation patch did not occur until egg laying had been in progress for several days. Some passerine birds begin defeatherization prior to the inception of egg laying (Bailey, *op. cit.*:125), but the difference in timing is undoubtedly related to the smaller clutch size of these birds. Refeathering of the breast usually occurred during the annual molt, but in one female (no. 560) 75 per cent of the contour feathers of the ventral tract were being replaced on June 14, 1952, prior to the normal season of the female annual molt.

Increased vascularization of the dermis (Bailey, *op. cit.*: stage II) seemed to follow closely upon the loss of the down feathers, but it varied considerably among females. At this time, the skin of the breast varied in color from pink to yellowish and was dry, flaky and wrinkled. The enlarged blood vessels were easily detected in a few of the birds but they were difficult to see in others. Quail incubation patches did not appear to be edematous nor did the thickness of the skin appear to increase, but no histological examination was made to verify this point.

Since male California Quail have been reported to incubate in the event of the disappearance of the female (Price, 1938), the breasts of the males also were examined at this season. One male only (no. 767) was seen to have lost feathers from the breast region but not to the extent seen in the females. This loss of feathers by a male might be due solely to wear during incubation. There was nothing comparable to the vascularized brood patch of females.

MOLT

Postjuvenal.—In quail, as in other galliforms, the replacement of the remiges, during the postjuvenal molt, progresses in an orderly sequence beginning with the proximal primary (no. 1) and ending with the replacement of primary no. 8. The molting of all other feather tracts is completed within this period of time. Dwight (1900:49) noted that the two distal juvenal primaries, numbers 9 and 10, together with the greater upper primary coverts, were retained throughout the first year. Petrides and Nestler (1943) described a method for determining the age of young Bobwhite based on the rate at which this wing molt progresses. Since their data were derived from captive quail of a different species, it was desirable to determine the applicability of their data to California Quail. The molt stage of all young quail captured more than once during one postjuvenal molting period on San Pablo Ridge provided the data for one of the replacement curves in figure 7. Since the precise age of these quail was not known, it was necessary to ascertain the age at which molt normally began in order to relate the curve to quail age.

Nineteen California Quail reared in captivity at Davis in the summer of 1954 provided the data for the second replacement curve. Because captive Bobwhites as well as captive Capifornia Quail were known to commence the postjuvenal molt at 28 days of age, the replacement curve for the wild quail was adjusted to the same datum point. The curve for Bobwhite was constructed from Petrides' data (*op. cit.*). Although the three curves do not differ significantly, the two curves for California Quail suggest the effects of captivity in retarding molt rate.

The tail molt offers a clue for the aging of young quail in the field, for a short period of time. Because tail molt in this species is centrifugal, the tail may appear "forked" in flight for a time after the beginning of the eighth week. The central feathers are dropped first, hence retention of the long outer juvenal rectrices is responsible for this appear-

ance. Young quail exhibiting this condition are usually between eight and eleven weeks of age.

Young quail in full juvenal plumage could not be sexed from appearance. By the sixth week of life, however, the appearance of the first few black feathers just below the eye in the cheek region was the first obvious indication of "maleness." New brown feathers in this region and at this age, were a slightly less obvious criterion for females. Male head plumes may be slightly longer, at an earlier age, than those of the females, but this is not an infallible key to sex recognition.

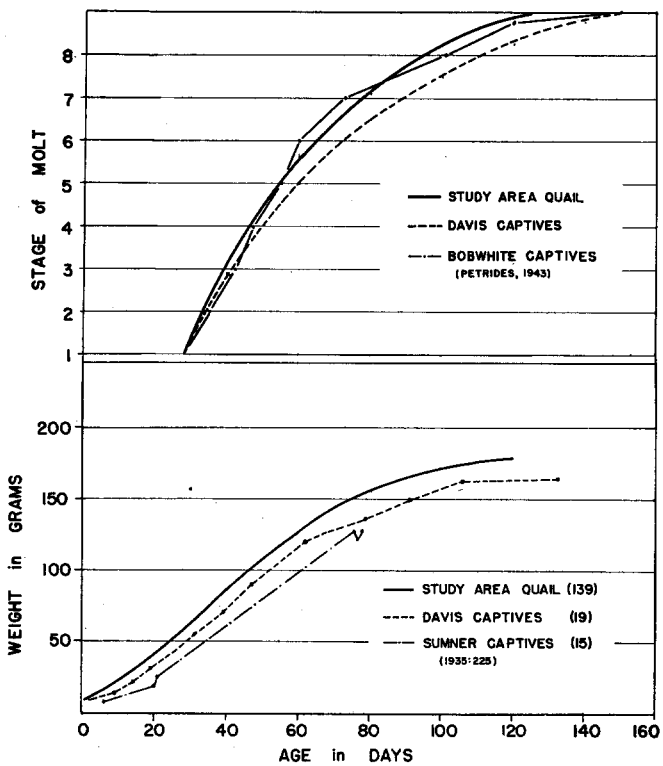


Fig. 7. Above, the postjuvenal molt. Molt stages correspond to the dropping of the juvenal primary of the same number. Below, growth curves.

Annual.—Unlike the postjuvenal molt, the annual molt of adult quail normally is complete. It resembles the postjuvenal molt, however, in that within the span of time required for the replacement of the ten primaries, the molting of all other feather tracts is completed. The stages of primary replacement, therefore, are a handy standard for comparison.

Figure 8 includes all the molt data for the three-year period. Male annual molt begins, almost invariably, in mid-June and is completed by mid-October. Sumner (1935: 250) apparently overlooked wing molt in observing that "the fall molt commences about the first week of August." The paucity of female records in the early stages of the molt is unfortunate, but by extrapolation, it is seen that they normally commence molting about one month later than the males. The extreme "scatter" of female records

seemingly reflects the frequent occurrence of renesting attempts (fig. 8) that would retard molt. Whether or not the females, once started, molt at a faster rate than the males, as indicated by the convergence of the two lines (fig. 8), is not clear. All females caught later than November 9 appeared to have completed their molt, as had the males. There was no clearcut relationship with age, or with success in breeding, in the timing of the annual molt in females. Paired and unmated males regardless of age likewise appeared to begin the annual molt at the same time.

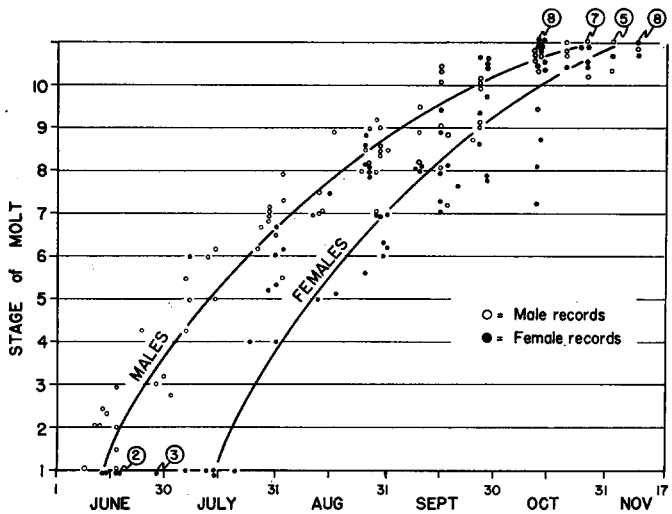


Fig. 8. The annual molt. Molt stages correspond to the dropping of the primary of the same number.

The similarity of the replacement rates of the postjuvenal and annual primary molts, together with the possibility that the inception of the female molt may coincide with the completion of brooding of young, suggests that the wing molt stage of a female and her brood might also coincide. One brood, reared in captivity by its two parents, lagged only six days behind the adult female in wing molt progression. Four wild females, on the study area, however, began molting from 16 to 36 days ahead of their "broods." It seems that the annual molt of females probably begins in the wild between the time of hatching of the young and the inception of their postjuvenal molt.

GROWTH AND WEIGHT

Growth of young.—No attempt to take linear measurements of wild juvenal quail was made, hence "growth," in this instance, is expressed as the increase in total body weight. The curve representing the fastest growth rate in figure 7 was obtained from the records of 139 juvenal quail captured in the three seasons of the study. The age of each individual was gauged from the stage of wing molt. Sumner (1935:225) earlier published a table of weight increases of 15 pen-reared quail that also appears in the form of an incomplete growth curve in figure 7 for comparison. Because of the objection of using the weights of quail whose age was not precisely known, additional data were obtained on the weight increases of 19 pen-reared quail at Davis in the summer of 1954 to serve as a further check.

The similarity of the three curves is obvious. While they represent the means of the growth-time relationship for each group, weight variability of each group overlapped

considerably. As one might expect, however, the wild quail appear to gain weight most rapidly, increasing at about two grams per day until they are nine-tenths grown. At this time, they are approximately three months of age. The fact that many of the captive quail lagged well behind the wild quail in gaining weight is undoubtedly a reflection of the necessity for eating that which was offered to them rather than being able to select their own food.

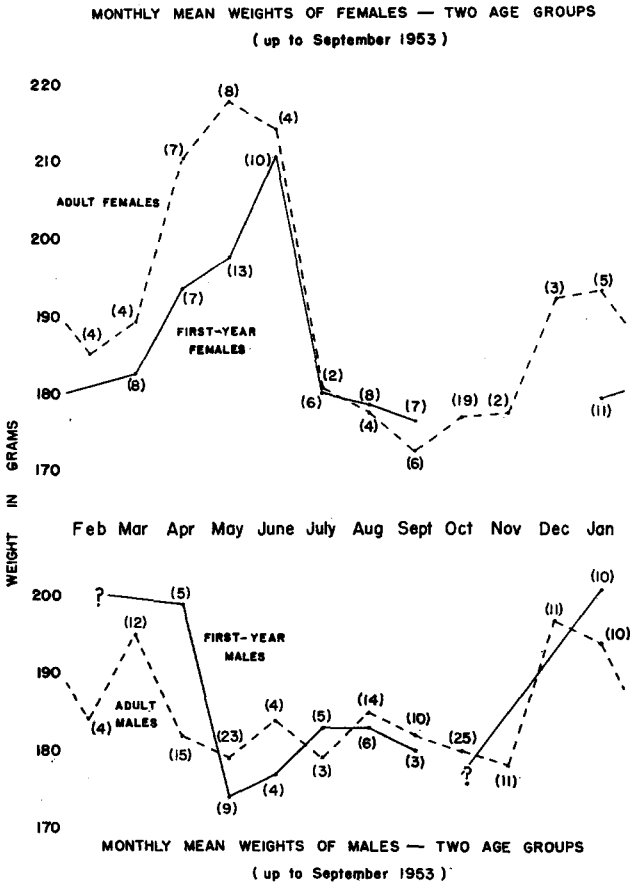


Fig. 9. Monthly mean weight curves. Numbers in parentheses represent sizes of samples.

Adult weight changes.—In figure 9, the monthly mean weights of more than three hundred live-trapped quail have been summarized. The records of first-year males and females were started in January, well after the period of rapid juvenal growth, and they followed through the first breeding season. Two peaks are present annually in the female weight curves. The first occurs during the breeding season and is thought to be coincidental with egg-laying. The lag in the weight increase of first-year females supports the earlier observation that these birds, by and large, commence laying slightly later than do the adult females. The early breeding season peak is followed by a rapid decline, supposedly induced by the stresses accompanying reproduction. The second rise in weight took place in all sex and age groups during the winter season. This increase

may be the result of the shift in diet (Sumner, *op. cit.*:178) that normally occurs at this season. November rains invariably result in the germination of annual grasses, which shortly become an increasingly important item of quail diet. Males undergo a sharp decline in weight in early spring. This may reflect behavioral changes associated with the pairing and fighting of the breeding season. Here, again, the first-year bird's weight change follows that of the adult.

SUMMARY

A three-year banding study (1950–1953) of the California Quail (*Lophortyx californica*) near Berkeley, California, provided the opportunity for observations on the annual behavioral patterns and physiological changes of these birds.

California Quail are monogamous but usually seek new mates each spring. Pair formation may be accompanied by a frontal display of the male before the female of his choice. The pairing birds appear to be able to recognize each other at an early stage of their relationship. First-year males rarely mate with older females, but older males mate as frequently with first-year females as with older females. Pairs composed of first-year birds were most abundant. The pair bond is strongly maintained by both members of a pair during the breeding season.

The function and seasonality of certain calls are considered. The date of the inception of "cow calling" was found useful in comparing the timing of three breeding seasons.

Threatening and fighting occurs between individuals at all seasons of the year. In the spring and summer these social interactions are most frequent and heated: paired birds fight off intruders to maintain their bond and to defend their young; unmated males fight to maintain territory in the vicinity of nesting pairs. In the fall and winter, fighting is concerned with the attainment and maintenance of social rank within the covey.

Testis size increases rapidly in March, reaches a peak by late April and regresses in July. Egg-laying begins by the second week in April and declines through June. The older females begin laying about two weeks earlier than the first-year birds. Defeatherization of the breast accompanies egg-laying in the female and is followed shortly by an increase in vascularization of the dermis to form an incubation patch. Males do not develop a comparable incubation patch.

The sequence of replacement of the primaries during the postjuvenal molt offers a useful clue to the age of the young bird. The sex of live "chicks" cannot be easily determined until the sixth week. The annual molt of adult males begins, almost invariably, in mid-June and is completed by mid-October. Females begin the annual molt after their young have hatched or about one month later than the males.

Young quail gain weight at approximately two grams per day until three months of age. All first-year and adult quail attain peak weight in midwinter. Laying females attain maximum weight while their mates are declining in weight.

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