

## BREEDING BEHAVIOR IN A POPULATION OF CALIFORNIA QUAIL

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The California Quail (*Lophortyx californica*) has been the subject of considerable investigation during the past 30 years, particularly from the point of view of management for hunting. Basic information on habits and general natural history was obtained by Sumner (1935). Subsequently, Glading (1938) made a nesting study of a population in the San Joaquin Valley; Emlen investigated population dynamics (1940) and movements (1939); and Emlen and Lorenz (1942) and Howard and Emlen (1942) studied social behavior, all in the Sacramento Valley.

In spite of these early studies, there has been a deficiency of basic information on density fluctuations, population turnover, productivity, movements, and social behavior in wild populations of the species. Therefore, in 1950, a study of the California Quail was initiated on an area of mixed chaparral-grassland on San Pablo Ridge, Contra Costa County, California. This investigation was conducted from 1950 to 1954 by R. E. Genelly (MS, 1955). The present study is a continuation of the same project, covering the period from 1954 through 1957. This paper presents findings of the latter four years concerning reproductive behavior in the population. Other facets of the work will be published separately.

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### STUDY AREA

The area on which the study was conducted lies on the east slope of San Pablo Ridge, Contra Costa County. It is about one-half mile north of Inspiration Point and the same distance west of San Pablo Reservoir. Most of the study was confined to a roughly rectangular tract about  $\frac{1}{3}$  by  $\frac{1}{2}$  miles, including approximately 100 acres. This area is equivalent to "Area A" as defined by Genelly (1955:264). His "Area B," on the west slope of San Pablo Ridge, initially was included; but early in 1955 the United States Army began construction of an installation north of the study area, and the dirt fire road that formed the core of "Area B" was paved and subjected to very heavy traffic, thereby rendering it unsuitable as a study area. Subsequently, the study was confined to "Area A."

The area drains to the east and is made up of three ridges and two intervening canyons, with chaparral and trees on the north-facing slopes, and grass on the south-facing slopes. The topography, vegetation, climate, and land-use of the area are described in detail by Genelly (1955:263-264).

## METHODS

*Trapping.*—The principal method of obtaining information was to capture the quail in traps, mark and release them, and then recapture them. The trapping effort resulted in 1062 captures of 444 marked birds.

Traps were made of one-inch mesh galvanized poultry netting formed into a rectangular box about two feet wide, four feet long, and two feet high. A small piece of the netting was formed into a short tunnel, semi-circular in cross section, which was inserted under one edge. The sides were fastened to the ground with spikes. Generally, traps were left in place and were set and unset by insertion and removal of the entrance tunnel. A mixture of small, whole grains, including a high percentage of millet, sold as "wild bird seed" by pet shops, was used as bait. Baiting and setting were done either in the early morning or in the late afternoon. Set traps were usually checked twice a day.

Fourteen trapping stations were utilized, but only ten were used regularly. They were all situated in locations established by Genelly, and I retained his numbering system (Genelly, 1955, fig. 1).

*Marking.*—A numbered leg band, obtained from the California Department of Fish and Game, was placed on each bird captured. Colored plastic numbered or lettered neck tags were attached to some of the birds for sight identification. These tags were identical to those developed and described by Genelly (*op. cit.*:265–266), who obtained valuable information by observation of birds bearing these neck tags, particularly in "Area B" where birds could be approached by car as they fed on the dirt fire road. Since the road was not used by quail after the first few months of this study and since the topography and vegetation of "Area A" permitted only infrequent observation of undisturbed quail, the application of these tags was discontinued after the second year.

*Data recorded.*—Age was determined by examination of the greater upper primary coverts (Sumner, 1935; Leopold, 1939). Juvenal birds were aged more precisely by noting the progress of primary feather replacement.

During the reproductive season the presence or absence of palpable eggs in the oviduct and the presence and degree of development of an incubation patch gave an indication of the stage in the breeding cycle of females.

Because of the difficulty of observing undisturbed quail on the regular study area, systematic observations of behavior were made of a covey of quail in nearby Tilden Regional Park. This covey regularly fed on lawns and in botanical gardens. Although the habitat was partly artificial, the behavioral phenomena observed in these birds in the park would probably be similar to those in the quail under more natural conditions on the nearby main study area.

## PAIRING

During the greater part of the year California Quail are highly gregarious. From late August well into March the birds remain in coveys, and their behavior is strongly directed toward the maintenance of these groupings. Howard and Emlen (1942) have elucidated some of the facets of covey behavior. Throughout the spring the tendency to aggregate becomes progressively weaker until, eventually, there is complete segregation into mated pairs and lone, unmated cocks. This breakup of the coveys has been described in general terms by Sumner (1935) and by Genelly (1955). In order to supplement these observations an opportunity was taken in this study to follow the pairing of the birds in a covey numbering about 40 birds in Tilden Regional Park. Periods of time were devoted to observation on March 20, 27, and 29; April 1, 3, and 8; and May 15, 21, 22, and 24, all in 1957.

On March 20, the birds fed and bathed in the dust as a group. There was no segre-

gation into pairs, and the only indication that the breeding season was at hand was an occasional short chase of one cock by another and one apparently unsuccessful attempt at copulation. A week later on March 27 there was a slight tendency for individual males and females to feed together, but probably there was shifting about, with different birds forming the loose male-female associations at different times. Hostile behavior in the form of short chases between two males or two females were frequent and occasionally seemed to involve the protection of a paired condition against an intruder. One act of copulation was observed between members of a pair isolated from the main covey.

By March 29 pairing had advanced considerably as evidenced by the fact that the covey, when frightened, scattered mainly in pairs and re-formed in part by the congregation of pairs. Thus, although most of the time was spent grouped in a covey, some pairs had been formed within the covey. Much hostile behavior was seen, particularly among the cocks, and chases occurred almost constantly. Two full-fledged "cock fights" were observed.

The social structure and behavior on April 1 had changed little. Observations on April 3, however, revealed definite segregation of some pairs for at least part of the time. No hostile behavior was displayed against a lone male that joined a feeding pair. By April 8 the birds still showed a tendency to aggregate, but they moved to and from the main group as pairs, and most of the time a pair or two were apart from the covey. An increase in hostile behavior was evidenced by the very frequent chasing, most of which involved two males.

Nearly complete segregation into pairs had occurred by the time of the next observation on May 6. However, the various pairs still remained together in a loose group, and even formed a tight, intermixed group while dust bathing. Four instances of copulation were observed, two within two minutes. Chases of one male by another were approximately as frequent as they had been a month previously. Behavior on May 15 was much the same as on May 6 with perhaps more frequent occurrence of completely isolated pairs. On May 21 and 22, however, there was little inter-pair association or association between pairs and lone cocks. Also, the lesser number of birds visible indicated that most pairs were occupied with actual reproductive activities such as laying and incubation. Covey break-up was thus essentially complete.

In summary, the beginning of pairing occurs in late March, with a slightly more frequent association within the covey of individuals with those of the opposite sex, with increased hostile behavior, and with attempts at copulation. Throughout April and May these behavioral changes are intensified, and by late May the pairs are engaged in reproductive activities. The striking feature of this pairing process is the length of time required for its completion in the entire covey. No observations were made of any particular "pairing" display. Edminster (1954:306) states that the pair bond is formed in the covey in an unobtrusive manner. Genelly (*op. cit.*:267) observed a display in which the male "rushed" the female with feathers spread and head down. This occurred when a male approached a female confined in a "cock and hen" trap. On the other hand, he describes an instance of pairing without obvious display by two birds separated only by wire netting. The indications of the present study are that the "rush" display does not figure importantly in pair formation.

#### HOSTILE BEHAVIOR

"Cock fights," chases, and other hostile behavior have been mentioned. Genelly (*op. cit.*:272) has discussed the seasonal variation in the frequency of fighting and finds that spring, including March, April, May, and June, is the time during which most hostile behavior occurs. Nearly all of my observations of hostile behavior likewise were made

in the spring. Behavior associated with the establishment and maintenance of a social hierarchy in winter coveys will not be considered.

Three types of hostile behavior are recognizable among California Quail during the breeding season. These are: chasing of one bird by another; actual fights, termed "cock fights" but occurring between females also; and a form of nudging by which one bird displaces another. There are apparently no elaborate displays serving to express hostile drives as are found in many birds (Moynihan, 1955).

*Chasing.*—The chase is probably the most basic of the three types of hostile behavior. It is certainly the most frequently observed. This behavior consists of the aggressor lowering its head, stretching its neck out toward another bird, raising the feathers on its head and body, and running toward the other. The attacked bird seems invariably to flee from the aggressor. Seldom does any vocalization accompany a chase unless it is the aftermath of a full-fledged fight. The distance covered in a chase varies from a few steps to many yards. A very short one may consist of a simple posturing by one bird followed by a few steps in retreat on the part of the other. A long chase may consist of a rapid rush by the aggressor followed by rapid running retreat by the pursued, with frequent dodging and even short flights by one or both birds. In these longer chases the pursuer seems actually to attack the other by pecking its nape. The commonest chase is one of a few feet, in which both birds run rapidly for several steps and then return to feeding.

The length and intensity of the chase appear to depend mainly on the aggressiveness of the pursuer. The pursued bird plays a passive role, merely attempting to escape the other. One observation, however, shows that such is not invariably the case. On May 5, 1955, two pairs and a lone male were feeding on a small patch of lawn in Tilden Park. The lone cock approached one of the paired females, and her mate made a rush as if to chase away the intruder. The latter did run away but persisted in attempting to approach the female. The chase then took a circular path around the female with the mated cock attempting to keep between his mate and the other cock and the latter attempting to keep away from his pursuer and get close to the female at the same time. On this single occasion the pursuing male gave several of the "squill" calls usually associated with genuine fights. After about one minute the intruding male desisted and was driven off. Although the chasing behavior is usually simple, with a clear-cut attack and retreat, resistance on the part of the attacked bird can complicate the pattern.

Chasing may occur as the result of hostility generated in several types of social conflict. The most common context is that of a bird defending its mate against an intruder. The intruder may be an unmated male or a member of another pair. Other situations leading to chasing are the close approach by a member of the same sex during preliminary pairing, conflict between two unmated cocks later in the season, and defense of young against adults or larger young. Two males are most often involved in chases, but the chasing of one female by another is common during pairing, and occasionally a male will chase a female. Genelly (*op. cit.*:272) reports a case of a paired female chasing away a lone male.

*Fighting.*—Actual fights involving physical contact occur in social situations similar to those described for chasing, but they occur much less often. These fights are similar to the battles of fighting cocks. The typical "cock fight" between two California Quail has been described as follows by Genelly (*op. cit.*:271): "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 adver-

sary. . . . 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." Fights begin by two birds walking erectly and rapidly toward each other. They commonly last but a few seconds, time enough for one to four leaps. The end result of a fight is the retreat of one of the contestants which is chased by his opponent for a short distance.

Although, as mentioned above, the "cock fights" occur in situations similar to those in which chases occur, the fights seem to be restricted to interactions between two birds of the same sex. No observations were made of fights between a male and a female. Most fighting occurs between two males, but occasionally fights between females were observed. In most cases the status of the cocks as to pairing was not known, but fights between two mated males and between two unmated males were seen. Whether unmated males fight with mated ones is not known, but it may be that unmated cocks are less aggressive and ordinarily flee when threatened by mated ones.

*Side-by-side nudging.*—The third type of hostile interaction between two quail is the side-by-side nudging. It is an inconspicuous type of behavior and was observed infrequently. This behavior appears to occur when one bird approaches too close to another bird or to its mate or young—that is, under conditions similar to those resulting in a chase. Again, males were observed to "nudge" more frequently than females.

Nudging consists of one bird approaching another one and taking a very close, side-by-side position. The two birds continue feeding, or at least pecking at the ground, but each one pecks at the ground under the head of the other. At the same time one seems to nudge or jostle the other one with its shoulder, presumably attempting to force it away. Body contact may be slight or more or less violent. Usually one bird gives ground slightly, and the two move apart and return to feeding in the normal manner. Calls were never heard accompanying this behavior. Nearly all of the observed instances of nudging were as subuded as described above, but on one occasion more aggressive behavior was involved. A male with a half-grown brood attempted to force a lone cock away from the area in which the family was feeding, and the lone male at first refused to retreat from the jostling parent. The latter then ceased pecking at the ground and began to peck at the nape of the other. The lone male ran away a few steps, and the parent returned to its family. In general, side-by-side nudging appears to occur in situations in which the birds develop less antagonism than that which results in fighting or chasing.

*Conclusions.*—Without further information it is impossible to draw many conclusions about the true functions and relative importance of these three types of hostile behavior. Especially needed are data of a quantitative nature and observations of marked birds the age and pairing status of which are known. It can be safely concluded, I believe, that fighting, chasing, and nudging express decreasing degrees of hostility in the order named.

#### COPULATORY BEHAVIOR

Copulation occurs throughout the period of pairing during the spring, probably beginning after preliminary pair bonds have been formed. In this study ten instances of copulation were observed; and the behavior was quite uniform and simple. In no case was any pre- or post-copulatory display given. Typically, the two birds foraged close together with the female leading. The female stopped feeding, settled into a low squatting position, and remained motionless. The cock, on observing the behavior of the hen, stopped feeding, straightened up, remained motionless for a very short time, and then

stepped forward and onto the back of the hen. Copulation was accomplished in a few seconds; the male stepped off and feeding was resumed immediately by both birds. In coition itself the female raised her tail into a vertical position; the male maintained his back in a nearly erect posture, bent his neck down, grasped the nape of the hen with his bill, and moved his pelvic region back and forth several times. Copulation may occur when a pair is isolated from the covey, but more often it was observed while other birds were feeding nearby. Only once was interference by other quail noticed. On May 6, 1957, a male dashed at a copulating pair, chased the other male about three yards, and remained near the female, feeding.

In the closely related Bobwhite Quail (*Colinus virginianus*) Stoddard (1931:17-18) describes a complicated "courtship" display performed by the male in front of the female preceding copulation. However, this display may function primarily in the formation of the pair bond rather than in preparation for copulation *per se*. The same may be said of Genelly's one observation of a display by a male California Quail toward a hen confined in a pen.

#### REPRODUCTION

The role of productivity in the dynamics of this particular population of quail will be discussed in a later paper, but special attention will be devoted here to the timing of certain phases of the reproductive process itself. A full study of reproduction would involve the collection of samples of birds of both sexes in order to examine their gonads and accessory structures. Unfortunately such collections could not be made in the present study because of adverse effects on the breeding population. Therefore, data on reproduction were obtained by examining birds trapped alive. Three main types of information may be gathered in this manner. First, it is possible to palpate shelled eggs in the uterus of the hens and to palpate soft, unshelled eggs if they are low enough in the oviduct. This method, taken from Genelly (1955:278), gives an indication as to the timing of the laying season. Another type of information is the presence or absence of an incubation patch. Possession of an incubation patch by a female is indicative of a later stage in the reproductive cycle than the presence of an egg in the oviduct. If enough hens are examined, the course of at least part of the reproductive cycle in the female population can be followed. The other phase of the reproductive cycle concerning which data were collected is the period of hatching. It is possible to estimate the ages of young quail if they are captured before they have completed the postjuvinal molt. If a sufficient number of such young birds is handled, the time of hatching of various broods can be ascertained.

Thus, by the examination of trapped birds during the breeding season, the course of laying, incubation, and hatching—on a population-wide basis—was followed. However, no information was obtained on the cycle in the males or on aspects of reproduction such as clutch size, nesting success, or hatching success.

*Laying and incubation.*—The reproductive status of all females examined in the breeding seasons of the four years of this study are summarized in figure 1. The solid bars represent adults, and the open ones first-year birds. A bird was considered to be laying if an egg was felt in the oviduct or uterus. Hens with no eggs but with an incubation patch were assumed to be incubating. Those without eggs were classified as "pre-laying" early in the season. It is nearly certain that each bird classified as "laying" was correctly listed, but there is likely to be error in classifying birds as "pre-laying" and incubating. Overlooking an unshelled egg in the oviduct or capturing a female soon after she had laid an egg must have occurred. Birds recorded as "pre-laying" in the third and fourth weeks of May would seem to be particularly suspect in this regard.

In spite of possible errors, the graphs do depict the course of events in the female

reproductive cycle. The graphs of Genelly (*op. cit.*:fig. 6)—from which the method of presentation used here was taken—show a very similar sequence of breeding events. Laying begins about the third week of April and continues into middle or late June. Incubation commences in the third week of May, and some birds appear still to be incubating in the first week of July. However, females incubating very late clutches were not captured, for the hatching dates of figure 2 (discussed in the next section) show that a few birds must still be incubating in late July and even into early August. Thus, the time spent by the females in various stages of reproduction lasts from mid-April through July, a period of over 100 days.

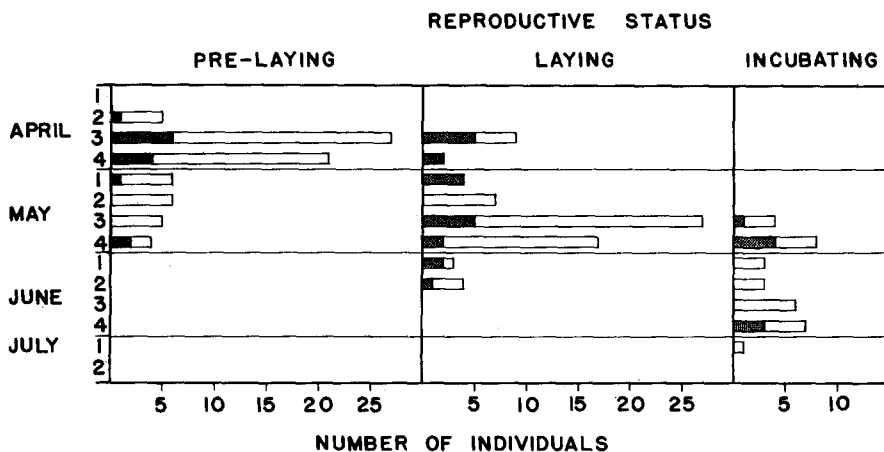


Fig. 1. Phases of the female reproductive cycle, based on data from four years. The stippled bars represent adult birds; the open bars are yearlings in their first breeding season.

If the data of figure 1 are segregated to show the pattern of each of the four years, certain annual variations may be observed. The dates on which an ovulating female was first observed were, respectively, May 5, 1954; April 14, 1955; May 1, 1956; and May 6, 1957. These dates are quite uniform except for the year 1955 when laying seemed to start much earlier than usual. Hatching dates presented in figure 2 likewise reflect the advanced date of breeding in 1955. Examination of weather records might be expected to reveal the cause of this difference, but neither precipitation nor temperatures were strikingly different in 1955. More data are necessary before the factors determining the onset of laying can be ascertained.

The dates of the cessation of laying are more uniform than are the dates of the beginning of laying. Only 14 days separate the extreme dates of the last laying hen as opposed to the 22 days separating the starting dates in 1955 and 1957. One inference to be drawn, therefore, from the dates of laying is that the earlier the population begins to lay, the longer will be its laying effort. It might further be presumed that, if laying occurs over a long period, the breeding effort would tend to be more successful. However, 1955, with a 50-day laying period, was less productive than 1954, with a 36-day period. Thus it can be concluded only that there is variation in the date of commencement of laying and that earlier seasons tend to be longer ones. What factors affect the time of laying, and what effect the length of the laying period has on productivity, are unknown.

*Hatching.*—The dates of hatching, shown in figure 2, were calculated from the esti-

mated ages of young birds captured alive. The method used to determine the chronological age of the juveniles is based on the uniform rate of maturation of the plumage and is described in a separate paper on plumage development. It is essentially the method of Petrides and Nestler (1943) and Genelly (1955:280). Most of the young birds were captured more than once, so that there is a check on the ageing in such cases. It will be seen in figure 2 that the first hatching dates in 1955 are earlier than those of the other years, as were the first laying dates.

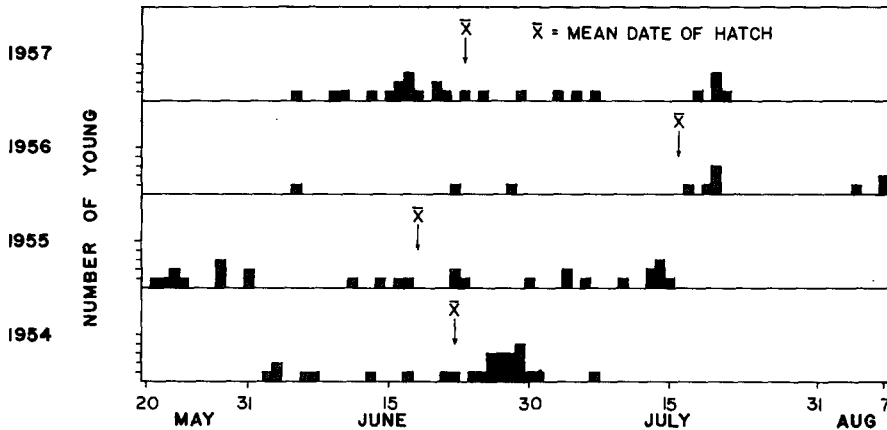


Fig. 2. Distribution of hatching dates in four consecutive years.

In 1956 three birds hatched near the end of the first week in August, two weeks later than the latest of the other three years. Genelly's data (MS) show a few late hatchings in August also. Such late hatchings are probably few in number and are the result of a belated effort to bring forth a brood by a pair that had failed once or twice earlier in the season.

#### SUMMARY

This paper presents observations pertaining to reproductive behavior in a population of California Quail in Contra Costa County, California. Pairing and covey break-up commenced in mid-March and were completed in May. Hostile behavior associated mostly with this period included chasing, fighting, and "side-by-side nudging." Copulation was observed several times and was uniformly simple and inconspicuous.

The periods of laying, incubation, and hatching varied from year to year in length and in time of commencement. However, in most years laying began about the third week of April and hatching ended in late July or early August, indicating a total breeding period of over three months.

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