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25 California Quail

Paul A. Johnsgard
University of Nebraska-Lincoln, pjohnsga@unlserve.unl.edu

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California Quail

Callipepla californica (Shaw) 1798
(*Lophortyx californicus* in *A.O.U. Check-list*)

OTHER VERNACULAR NAMES

CALIFORNIA partridge, Catalina quail, Codorniz Californiana, crested quail, San Lucas quail, San Quintin quail, topknot quail, valley quail.

RANGE

From southern Oregon and western Nevada south to the tip of Baja California. Introduced into southern British Columbia, Washington, Idaho, northern Oregon, and Utah.

SUBSPECIES (*ex A.O.U. Check-list*)

C. c. californica: Valley California quail. Resident from northern Oregon and western Nevada south to southern California and Los Coronados Islands of Baja California. Introduced in eastern Washington, central British Columbia, western Idaho, Oregon, Utah, and Colorado.

C. c. catalinensis (Grinnell): Catalina Island California quail. Resident on Santa Catalina Island and introduced on Santa Rosa and Santa Cruz islands, southern California.

C. c. plumbea (Grinnell): San Quintin California quail. Resident from San Diego County, California, through northwestern Baja California, Mexico.

C. c. achrustera (Peters): San Lucas California quail. Resident in southern Baja California, Mexico.

C. c. canfieldae (van Rossem): Inyo California quail. Resident in Owens River valley in east central California.

C. c. orecta (Oberholser): Great Basin California quail. Resident in the Warner Valley, southeastern Oregon.

C. c. decoloratus (van Rossem): Baja California quail. Resident in Baja California from 30° north latitude to about 25° north latitude.

C. c. brunnescens Ridgway: Coastal California quail. Resident in the humid coastal area of California from near the Oregon boundary south to southern Santa Cruz County. Introduced on Vancouver Island, British Columbia.

MEASUREMENTS

Folded wing: Adults, both sexes, 105–19 mm (males average 5 mm longer than females).

Tail: Adults, both sexes, 79–119 mm (males average 4 mm longer than females.

IDENTIFICATION

Adults, 9.5–11 inches long. The sexes are different in appearance. This widespread quail of the western foothills resembles the Gambel quail inasmuch as both sexes have forward-tilting, blackish crests that are enlarged terminally into a "comma" or "teardrop" shape. Both sexes also have clear bluish gray to gray chests that become buffy toward the abdomen and have darker "scaly" markings reminiscent of scaled quail. The flanks are brownish gray with lighter shaft-streaks, and the upperparts are generally gray to brownish gray, intricately marked with darker scaly markings. Males have black throats and a chestnut-tinged abdomen and are chocolate brown behind the plume, while the area in front of the eyes and above the bill is whitish.

FIELD MARKS

The combination of a "teardrop" crest and scaly markings on the lower breast and abdomen is distinctive for both sexes. Males of this species may

be distinguished from the very similar Gambel quail by the combination of a whitish rather than blackish forehead, no black abdomen patch, and dull brown rather than chestnut brown flank and crown coloration. A three-note *chi-ca-go* call serves as a location call for both sexes.

AGE AND SEX CRITERIA

Females have dark brown rather than black crests and lack black throats.

Immatures have buff-tipped upper greater primary coverts which are carried for the first year (Sumner, 1935; Leopold, 1939), and the outer two primaries are relatively pointed and frayed. Maximum width (but not length) of the bursa of Fabricius may be used as an accurate indication of immaturity through December (Lewin, 1963).

Juveniles resemble females but have forehead feathers with indistinct pale grayish terminal spots and have shorter and lighter crests (Ridgway and Friedmann, 1946). See Gambel quail account.

Downy young (illustrated in color plate 110) are very difficult to distinguish from young Gambel quail (see that species' account), but they can be recognized from downy scaled quail by their less grayish white and more yellowish body tones, and by the fact that the pale spinal stripe in the California quail is cinnamon-buff rather than a dirty brownish buff. This species is considerably lighter and more yellowish on the lower back and tail than downy elegant quail.

DISTRIBUTION AND HABITAT

The California quail exhibits a rather complex distribution pattern that extends along the western coast of North America for about two thousand miles, from the southern tip of Baja California, Mexico, to the southern part of Vancouver Island, British Columbia. Along this entire range its coastal distribution is almost unbroken except for forested areas associated with the Coast and Olympic ranges. The climatic and precipitation variaations along this coastal strip are considerable, ranging from hot scrub desert along much of Baja California, through a mild Mediterranean climate associated with chaparral vegetation in southern California and a cool, wet coastal forest (where the bird occurs in edge and successional vegetation stages) from central California northward to Puget Sound. In the interior of these coastal states, as well as in Nevada, Idaho, and Utah, the species also occurs in valleys and rain-shadow areas dominated by grasslands or semidesert sagebrush shrub, although many of these interior populations are introduced ones.

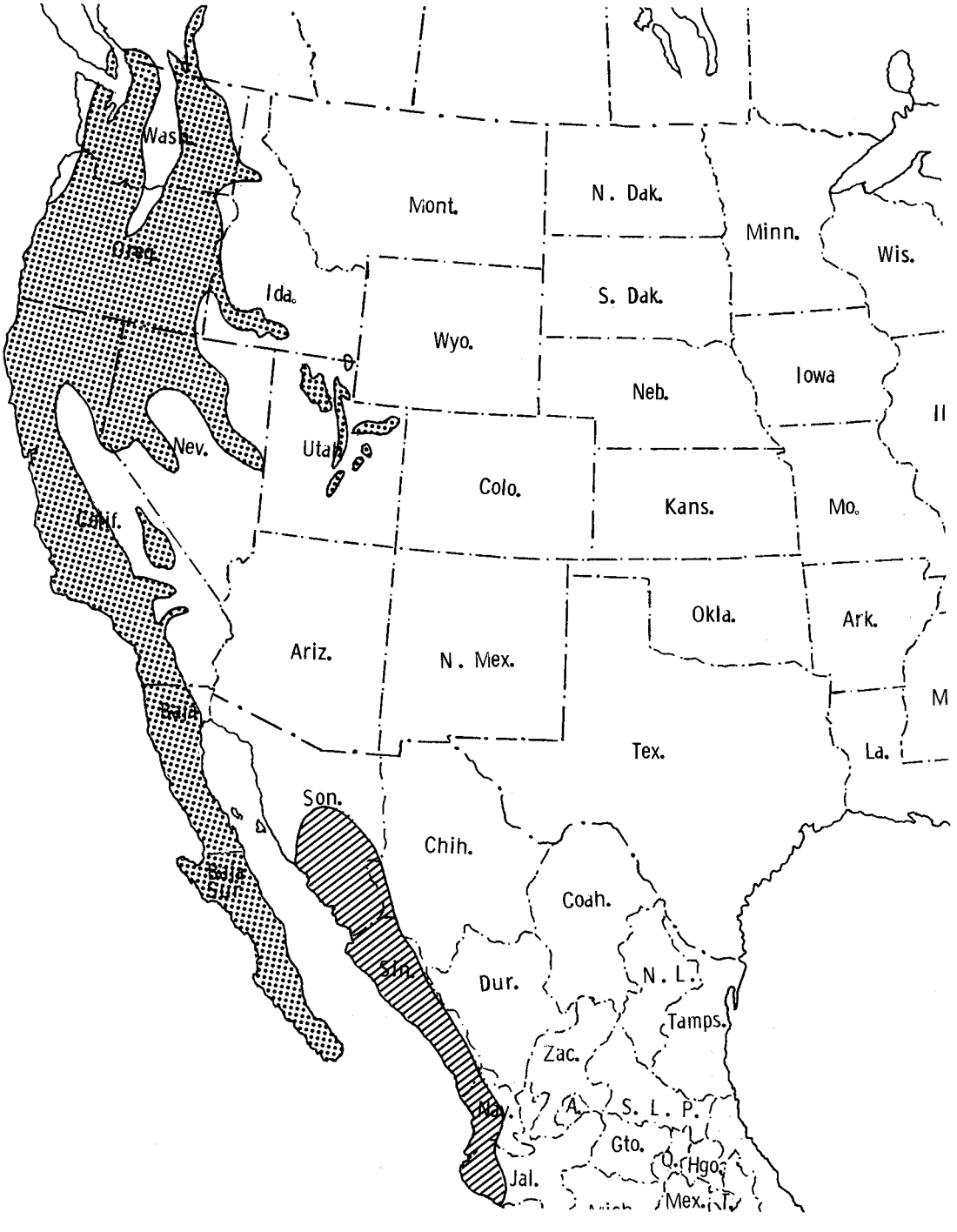

FIGURE 38. Current distributions of the California quail (shaded) and elegant quail (hatched).

In Mexico, Leopold (1959) reported that the highest populations are found in chaparral vegetation along the northwestern Baja coast and foothills and in scrubby tropical forest and brushland at the tip of the San Lucas Cape, but they also occur in desert washes wherever there is a combination of brushy cover and water available.

In California several races occur, but all are associated with brushy vegetation in combination with more open weedy or grassy habitats and available water supplies. Heavy forest and dense chaparral is avoided even by the coastal race, although dense-foliaged trees may be used for night roosting. The exact vegetational composition is probably not so important as life-form characteristics of the dominant vegetation, namely an interspersion of brush and more open vegetational types (Grinnell and Miller, 1944).

In Oregon the species was probably originally confined to the counties bordering California (*californica*) and Nevada (*orecta*), but trapping and transplanting activities have spread the bird's range to most of eastern Oregon and many western Oregon counties, with consequent mixing of subspecies stocks (Masson and Mace, 1962). The highest populations occur in the Columbia basin and in central and southeastern Oregon, in dry, semidesert vegetation.

The Washington population of California quail is likewise largely or entirely an introduced one, of uncertain subspecific designation. Its preferred habitat is thickets, brushy tracts, logged areas, and burned over districts, and although sometimes seen in second-growth timber it avoids heavy woods (Jewett et al., 1953).

In Canada the California quail is generally limited to one small introduced population on the southern part of Vancouver Island and another in the Okanagan Valley (Godfrey, 1966; Lewin, 1965). More is known of the Okanagan and Similkameen valley populations than the island population, and Lewin reported that about 390 square miles of these river valleys are occupied by an estimated population of about 250,000 quail. The quail are associated with orchards and irrigated areas and are generally found below two thousand feet elevation. A few also occur in native vegetation consisting of scattered thickets of aspen (*Populus*), rose (*Rosa*), Saskatoon berry (*Amelanchier*), and chokecherry (*Prunus*), but they do not extend into the higher coniferous woods (Lewin, 1965).

In Idaho the species occurs locally along watercourses of the Snake River valley from near the middle of the state to the Oregon line, and a limited population also occurs along the Snake and Clearwater rivers in northern Idaho and perhaps in the Clarkia and upper St. Joe river valleys as well (Upland Game Birds of Idaho).

In Nevada the range of the possibly originally native California quail has been greatly affected by release programs, but the birds are usually associated with rose and willow thickets along streams, where cover and water are both available. In western Nevada the heaviest populations occur in agricultural areas, but the birds are found wherever springs exist. In eastern Nevada their distribution is limited and spotty (Gullion and Christensen, 1957).

In Utah the species was first introduced over a century ago and thus is now found in scattered areas around the state, but it is primarily limited to semiarid foothills and valleys, especially along streams (Rawley and Bailey, 1964). An introduced population once occurred in north central Colorado, but now is wholly extirpated.* Recent attempts at establishing the species in Arizona may have been successful in the vicinity of the Little Colorado River near Springerville, but it is too early to be certain of this.

POPULATION DENSITY

Population densities doubtless vary considerably in this species according to habitat quality. Emlen (1939) reported on a "low density" winter population that contained 113 birds on a study area that represented a density of 1 bird per 7 acres. However, if only the occupied home ranges of the birds were considered, the four coveys' total occupied area was 93 acres, or 0.9 acres per bird. Raitt and Genelly (1964) reported on a population that also contained four winter coveys on approximately 100 acres. Over an eight-year period this area had fall populations ranging from 25 to 140 birds and averaging 101 birds, or 1 bird per acre. Since the average fall age ratio was 1.47 juveniles per adult, the average spring breeding population (ignoring spring to fall adult mortality) must have been at least 41 adults. Thus a spring breeding density of approximately 1 bird per 2 acres would seem probable. These figures are in general agreement with those of Glading (1941), who recorded late winter densities on a study area in central California that varied over a six-year period from 1.7 to 3.9 acres per bird.

Maximum population densities that have been noted for the species are some reported on a private hunting club property where artificial feeding and predator control measures were used, and fall populations of up to 4.8 birds per acre were attained (Glading, Selleck, and Ross, 1945).

HABITAT REQUIREMENTS

A fairly detailed analysis of habitat needs of the California quail has

*Glenn Rogers, 1970: personal communication.

been made by Emlen and Glading (1945). They classified quail habitat into four general types, desert, range land, dry farming land, and irrigated land, of which the range land is most extensive and most important to the species. Within these general categories, the basic habitat requirements of food, water, escape cover, roosting cover, nesting cover, and loafing cover are variably available. Irrigated lands provide water but may be limited in the various cover types, especially for roosting, nesting, and loafing. Dry-land farming areas are even less suitable, since they may lack available water in addition to escape cover or other cover types. Deserts usually provide both food and cover sources, and if water is locally available, they may support moderately large quail populations. Range lands vary greatly in quality of habitat, but the best offer available water, seed-producing herbaceous plants, and moderately open brushy cover that will serve for escape, nesting, roosting, and loafing.

Edminster (1954) has analyzed the aspects of cover that are most desirable for quail usage. Nesting cover is usually herbaceous rather than brushy, in a moderately open situation. Roosting cover is provided by tall shrubs or trees, with evergreen species being preferred for winter cover. Escape cover consists of dense growths of shrubs, vines, or herbaceous growth into which the birds can readily run when frightened. Feeding cover is usually not limiting, since the birds consume a large variety of seeds, but leguminous plants are preferred both for seeds and their leafy growth, perhaps because of their nitrogen content. Loafing cover consists of shady places under shrubs or trees, where relief from the midday sun is available and dry dust as well as grit may be readily available. The California quail depends more on available water or succulent plant material than does the Gambel quail, but it is more drought tolerant than the bobwhite (McNabb, 1969). Probably as long as insects and succulent vegetation are available the bird can survive indefinitely without surface water, and moderately saline water sources (but not sea water) can also be utilized (Bartholomew and MacMillen, 1961).

FOOD AND FORAGING BEHAVIOR

The animal portion of the diet of California quail is relatively small and even during summer probably contributes no more than 5 percent of the diet of adults (Martin, Zim, and Nelson, 1951; Edminster, 1954). Otherwise, nearly the entire remainder of the diet consists of herbaceous leafy materials and seeds, with grains and fruits playing a very subsidiary role in most areas.

Edminster (1954) summarized much of the early food studies of California

quail and concluded that the most important food sources were legumes (25 to 35 percent of all foods taken) and annual weeds (20 to 60 percent), followed by grasses (10 to 25 percent) and the fruits and leaves of woody plants (3 to 5 percent). Of the important legumes, bur clover (*Medicago*), lupines (*Lupinus*), deervetches (*Lotus*), clover (*Trifolium*), acacias (*Acacia*) and vetches (*Vicia*) are major food sources, especially their seeds. The leaves and seeds of filaree (*Erodium*) and the seeds of turkey mullein (*Eremocarpus*) are important food sources among the weedy herbs (Edminster, 1954; Martin, Zim, and Nelson, 1951).

Two more recent California studies confirm these earlier conclusions as to the significance of legumes for this species. Shields and Duncan (1966) found that during the fall and winter, seeds comprised over 80 percent of the bird's diet, with four species of legumes (*Lotus, Lupinus,* and *Trifolium*) alone making up 60 percent of the sample volume. With the start of the winter precipitation, the intake of leaves increased from 6 percent of the diet in November to 41 percent in January, with the leaves of forbs, clover, and grasses all being utilized. The importance of legumes was also pointed out by the study of Duncan (1968), who compared the foods taken during fall in burned and unburned rangeland. Relatively little difference in the two habitat types was found, with seeds from five species of *Lotus, Lupinus,* and *Trifolium* again making up from 66 percent of the early fall diet in unburned areas to 80 percent of the diet in burned areas. Among non-legumes, filaree and turkey mullein were important seed sources.

Food studies from areas outside the California quail's native range are more limited and suggestive of greater dependence on nonnatural food sources. In Nevada a considerable utilization of grain crops, such as wheat, barley, and corn, as well as the legumes alfalfa and sweet clover, is indicated by Martin, Zim, and Nelson (1951). In eastern Washington, Crispens (1960b) found that wheat seeds were the most important source of food throughout the year. Seeds of various weedy species, such as pigweed (*Chenopodium*), teasel (*Dipsacus*), and locust (*Robinia*) were selectively utilized, and both sunflower (*Helianthus*) and Russian thistle (*Salsola*) were highly preferred food sources. Surprisingly, legumes were found in very limited quantities among these samples.

The general lesson to be obtained from these studies is that the need for brushy habitat by the California quail is largely a reflection of its protective cover requirements, while most of its food sources come from herbaceous forbs, particularly legumes.

MOBILITY AND MOVEMENTS

Emlen's study (1939) of California quail movements is still the most

complete and will be summarized here. During the winter, the birds occupied home ranges roughly comparable to the size of the covey, with four coveys of twenty-one to forty-six birds using home ranges of seventeen to forty-five acres. These covey locations were associated with the distribution of brushy cover such as shrubs, perennial weeds, and vineyards. Each covey tended to feed together but sometimes broke up into smaller feeding units. Usually the birds of a covey roosted together but sometimes used two or three roosting sites. The coveys were separated by distances of from 350 yards to a half a mile, and contacts between coveys were thus infrequent. However, during such intercovey contacts, a "social barrier" between members of the two groups existed, which virtually prevented any covey shifting. Winter movements were very restricted, with rarely more than a fourth or at most a half of the covey's home range being used during any single day. Over a period of time, however, the birds would feed in different parts of the covey's home range.

Beginning in late February, coveys began to break up as pairs and unmated males began to break away from the group and apparently moved into more open farm land that was not suitable for winter use because of its limited cover. About half of sixty-seven marked birds separated from their coveys by the first of April, and the birds which left were predominantly males. At least one male moved a mile and a half before the nesting season. Further, younger males were evidently more inclined to leave the covey than older ones, since fourteen of the twenty-one males that disappeared were young. Only one of the twenty-one young males remained to nest on its winter territory, while seven of eighteen older males did so. Likewise, the young females tended to leave the winter range, while the adult hens all remained in the covey. By the middle of April the covey was composed of a nearly balanced ratio of the sexes and apparently consisted largely of older and mated birds. The second phase of covey breakdown was caused when these birds dispersed for nesting. Only a few nonnesting or late nesting birds remained around the winter roosting sites.

Movements during the summer were highly restricted and were largely limited to those of unmated males. These birds began to *cow* call in late April with the start of the nesting period and would attempt to approach females of mated pairs. Of eight such birds, four established "crowing territories" near the nest of an established pair, while the others assumed a more nomadic existence, sometimes covering a mile in a single day. Later, Genelly (1955) discovered that most such territories are held by old males, while the first-year males are principally nomadic. On the other hand, mated pairs limited their daily moves during egg-laying to from twelve to twenty-five acres while foraging, and returned at night to a roosting site, sometimes held in common with a neighboring pair. When incubation began,

movements were even more limited, to about three to ten acres around the nest.

Many nesting attempts were unsuccessful, and losses of a member of the pair caused some shuffling. If a mated male was lost, the female soon mated with one of the unpaired "crowers" near the nest or became foster parent of an available brood. When males lost their hens they started crowing within a day, either at the same place or at distances from one-fourth to one and one-half miles away from the original nesting location.

With the hatching of young, the re-formation of coveys began, with broods forming covey nuclei. By the middle of August, nine such covey nuclei had been established, and these attracted individual nonbreeders or unsuccessful breeders, so that the covey sizes gradually grew. Brood mobility was very low during the first few weeks of life, probably being limited to a few acres, but they ranged up to ten or twenty acres by the end of the first month. Some older broods moved considerable distances when their brooding cover was destroyed, with one brood of ten-week-old chicks moving a mile from its point of hatching. However, most broods remained close enough to the nest site that they wintered on the covey home range nearest their place of hatching. Although little interbrood shifting occurred in very young broods, this increased after the young were three or four weeks old, and the adults would tolerate the presence of other chicks of the same age. Contacts became more frequent when the chicks were somewhat older, and soon mergers of broods occurred, with nine broods gradually being incorporated into six subcoveys.

The subcoveys retained their identities until late November, when they condensed into four coveys that exhibited ranges nearly identical to those held the previous winter. Eight of twelve marked birds returned to the winter range held the previous year, while four occupied new winter ranges, but in all probability less than half of the total number of adults returned to their previous winter ranges.

A more recent study by Genelly (1955) supported Emlen's view that the dominant, nesting territory-holding males are usually older birds, while the nomadic and unmated ones are primarily young birds. It would seem probable, therefore, that population dispersion and range extension would be primarily the result of movements by young birds, especially males. Lewin (1965) mentions a report of a male being seen during midsummer some twenty-two miles north of regularly inhabited range. Also, when birds have been released into new areas considerable movement sometimes occurs; Richardson (1941) noted several such movements in excess of twenty miles and one extreme case of a ninety-five-mile movement.

On the basis of movements of recaptured birds at various trap sites,

Raitt and Genelly (1964) obtained an index of relative mobility, which suggested that summer and winter movements are least, while spring and fall movements are more extensive, particularly during April and May. These observations tend to support Emlen's views that a good deal of individual movement occurs in spring, especially among males. Although fall mobility is also moderate, there is little interchange of covey members at this time, thus a "spring shuffle" rather than a "fall shuffle" may tend to bring about population mixing.

SOCIAL AND REPRODUCTIVE BEHAVIOR

The covey is the social unit of the California quail from late fall until early spring. Emlen (1939) and, later, Howard and Emlen (1942) have pointed out quite clearly that in the California quail the covey is a relatively closed social unit, with little opportunity for intercovey mixing. This mixing is reduced or prevented during late winter and spring by attacks on outsiders by resident birds of the same sex; such established covey members always socially dominate aliens that are introduced into a covey. However, Howard and Emlen emphasized that this aggressive behavior should not be considered territorial defense by covey members but rather a form of social dominance associated with confidence related to the residents' knowledge of the local range. Territorial behavior in the sense of a defended area does not occur in coveys or mated pairs of this species (or probably any New World quail); only some unmated "crower" males exhibit anything like proprietary behavior toward a specific piece of habitat.

The process of covey breakup and pairing has been well studied in this species, first by Emlen and later by Raitt (1960) and Genelly (1955). Perhaps because older males begin their reproductive development somewhat sooner than younger ones, pairing that occurs prior to covey breakup involves primarily older males, which mate with both adult and first-year females. Such pairing probably begins in late February or early March, and during early stages of pair formation some shifting about of partners may occur. Most pairing occurs before the testes are much enlarged (Anthony, 1970), thus pair formation does not necessarily involve copulation or other strong sexual behavior patterns on the part of the pair, although copulation attempts may occur. Genelly (1955) felt that an initial stage of "acquaintanceship" might be required, during which individual recognition develops. No striking displays need occur in association with pair formation (Raitt, 1960), and only rarely is the "rush" display of males seen. Genelly (1955) mentioned seeing it only when females were placed in traps, and I have seen it only when a female was introduced without prior contact into the

cage of an unmated male. The display consists of several low notes followed by an extension of the neck and a lowering of the head, a fluffing of body feathers, a raising and spreading of the tail, and a slight extension and marked drooping of the wings, so that the primary tips touch the ground. In this posture the male approaches the female in a series of short rushes, from which the hen typically flees. The highly aggressive origin of the display may be seen from the similarity of it to threat postures assumed toward other males and the actual pecking attack that the male may perform on the female if she is unable to flee. In short, the display appears to be a strong assertion of dominance, and probably only the submission behavior of the female and her lack of male plumage features normally inhibits overt attack.

As the males and females of incipient pairs begin to remain with one another an increasing amount of time, male-to-male aggression also increases. This probably largely involves a chasing of other males from the vicinity of the mate, and an eventual exclusion of such unmated males from the covey. Since the sex ratio of spring coveys always has an excess of males, a forcible exclusion of surplus males is the only way that the covey can remain intact and persist as an integrated social unit. Raitt (1960) noted three major forms of hostile behavior: side-by-side nudging, chasing, and overt fighting. Nudging is the least aggressive of the three, and sometimes occurs among members of a pair or between adults and young, with the dominant bird pushing the other to one side as they both jostle for a common food source. Chasing consists of a posture much like that mentioned as typical of the "rush" display, but somewhat less extreme form. The bird being chased usually flees on foot and if caught may be severely pecked on the back and nape. Most often, such chases involve two males, but sometimes females chase females, and less frequently males will chase females. One case of a mated female chasing away an unpaired male has also been noted (Genelly, 1955). Overt fighting is virtually limited to males and is essentially like that of other quail, with the two birds facing one another, making pecking attacks and short vertical leaps during which they attempt to peck the top of the opponent's head. Between attacks, a series of *squill* calls and associated rapid head-throws that maximally expose the black throat are frequent and no doubt serve as major visual and acoustical threat signals.

Genelly (1955) noted a continued increase in fighting incidence from January until May, with this rise largely reflecting fighting concerned with the defense of the mate. Defense of territory occurred only from March through June, and consisted of fights among unmated males that had established crowing territories and subsequently repulsed other such males.

Starting in July, fighting associated with the defense of the brood occurred, but by October all of the fighting, which gradually diminished until January, was concerned with peck order establishment in the fall and winter coveys. Genelly could find no evidence that California quail actively defend a nesting site, thus the term "nesting territory" is not appropriately applied to the species.

As the mated pairs gradually break away from the covey and locate nesting sites, unpaired males attempt to establish crowing territories in the vicinity of such mated pairs. Genelly first heard *cow* calls uttered by these males in March, and the calling persisted until mid-June. This period corresponds roughly to the period of testis growth plotted by him. The greatest concentration of crowing males was located where nesting pairs were also located. Genelly found only one instance of a mated male uttering a *cow* call and heard a captive female produce it on at least two occasions, so the clear function of the call is that of advertising the location of a sexually active, unmated male. Since laying females that lose their mates through death rapidly attain new mates, the biological advantage of crowing is readily important. However, the localization of crowing males in the vicinity of nesting females may tend to increase the predation rate on such nesting birds.

The gonadal cycle of the female lags about two weeks behind that of males during spring (Genelly, 1955; Anthony, 1970), with adult females either developing slightly in advance of young ones (Genelly) or at approximately the same time (Anthony). Egg laying during Genelly's study in California started the second week of April, with a peak activity the third week in May, while in eastern Washington the peak of laying activity was about a month later, according to Anthony. The rate of egg laying is about 5 per week, at least in captive birds (Genelly, 1955), and the eggs are apparently usually dropped about midmorning. The average clutch size has been reported as 10.97 eggs by Glading (1938b), 13.7 eggs by Lewin (1963), 13.7 (in New Zealand) by Williams (1967), and 14.2 eggs by Grinnell, Bryant, and Storer (1918). Thus, an average figure of 14 eggs in a complete clutch would seem to be a reasonable judgment, which might thus require a total of about twenty days to lay; this plus an additional twenty-two-day incubation period would total forty-two days from the laying of the first egg to the day of hatching (Lewin, 1963). My incubation records indicate that twenty-two or, more commonly, twenty-three days may actually be required for incubation under artificial conditions.

Although renesting is a regular aspect of California quail behavior, the question of the frequency of second broods is not yet fully resolved. Definite instances of second broods have been recorded; McLean (1930) found one

such case in a wild bird. Francis (1965) also reported two cases of confined quail in which the male took over the care of the young after about two weeks, when the female remated and began a new clutch, which was subsequently hatched and raised. McMillan (1964) noted that early nests and broods of quail were being cared for by males, while females were presumably freed to raise additional broods. Finally, Anthony (1970) noted that during June and July a larger number of broods were tended by lone males than during August and September, suggesting either that there was high early female mortality or that females left the early broods in the care of males and went on to produce second clutches, the latter of which he believed to be the case. Incubation by males is probably not a regular feature of California quail behavior as long as the female is present; they do not exhibit highly vascularized brood patches as do females (Genelly, 1955). The visual stimulus of an abandoned clutch of eggs may bring about hormonal changes in males that initiate brooding behavior and defeathering adequate to form a simple brood patch (Jones, 1969b).

Broodless males, such as those who have lost their mates, have great interest in young chicks and, if admitted by the parents, make excellent foster parents (Emlen, 1939). However, although crowing males exhibit extreme interest in young broods, they are not allowed to tend them as long as they persist in their crowing behavior, according to Emlen. Parents and chicks gradually merge with unsuccessful adults and eventually with unmated males and with other well-grown broods, forming moderately large aggregations of birds.

Although the percentage of unsuccessful nesting attempts is high in California quail, the combination of persistent renesting, large clutch sizes, and occasional double-brooding usually assures a high ratio of young birds in fall coveys. Nesting losses have been estimated by Sumner (1935) to be about 60 percent, and other studies such as those of Glading (1938b) have revealed losses as high as about 80 percent. In New Zealand, Williams (1967) reported a fairly high nesting success of 62.6 percent, if only nests with completed clutches were considered rather than all indications of nesting attempts being considered. His figures also indicate a fairly high incidence of egg fertility (93.8 percent) and hatchability of fertile eggs (89.8 percent). Anthony's studies indicate a surprisingly high survival rate of chicks, with an estimated 25.8 percent mortality during the first fifteen weeks of study. Edminster's review of other studies (1954) suggests that a chick loss of about 45 to 50 percent may be normal. Over an eight-year period, the yearly fall age ratio of a quail population studied by Raitt and Genelly (1964) varied from 0.56 to 2.22 immatures per adult,

or a yearly average of from about one to five young reared per adult female, allowing for a somewhat unbalanced sex ratio in adults. Perhaps an over-all average fall age ratio would be about 1.46 young per adult (Emlen, 1940), or about three young raised per female.

Vocal Signals

A complete analysis of the vocal repertoire of the California quail has recently been provided by Williams (1969), whose terminology will in general be followed here.

Social integration calls include the contact call or *ut, ut* notes and the separation ("assembly") *cu-ca-cow* call. The *ut, ut* notes serve to keep individuals of a group in contact and are given frequently as the birds move about while foraging. When birds are separated visually, they may utter the call in a louder version, but it soon leads to the *cu-ca-cow* call. This loud, somewhat melodious call (sometimes written as *chi-ca-go*) is produced almost identically by both sexes, although there is a certain degree of individual variation in the call. Thus, males can definitely recognize the call of their own mates and will preferentially respond to them. Besides serving as a general separation call the *cu-ca-cow* plays an important role in reproduction, by serving to keep the pair together. In spring the call increases in frequency even in birds that are not separated, when unpaired birds of both sexes begin to use it. However, paired females do not use it unless separated from their mates, and unpaired males soon change from this call to the *cow* crowing call described earlier. This call is much like the last syllable of the separation call, but is uttered from a conspicuous, usually elevated, position. The call is repeated fairly often, averaging from about three to eight per minute. Williams established that the rate of *cow* calling was under testosterone control and was associated with relative aggressiveness. Thus the functional and hormonal origin of the call and the associated establishment of crowing territories is analogous to the territorial behavior of unmated male songbirds.

The *squill* call (called the "sneeze" by Williams) was so named by Sumner (1935), who described it as a high-pitched staccato whistle, used in a situation of defiance to other males. The call is limited virtually entirely to males and occurs only during the breeding season. Somewhat in contrast to the related *meah* call of the Gambel quail, its utterance does not indicate a mutual "stand-off," but rather it is associated with extreme threat and attempted social dominance. The neck-stretching caused by the head-throw raises the pitch of the vocalization to a near whistle, no doubt because of the increased

tension on the tympanic membranes. A second aggressive call of the male is the *wip, wip* call which often precedes attacks on other males and may alternate with the *squill* call. It may also be uttered toward strange females, but I have never seen a male perform a *squill* call toward a female. Likewise, the *wip, wip* call has not been reported for females, which utter only *ut, ut* or *cu-ca-cow* calls in this situation.

When feeding, California quail utter soft and repeated *tu, tu* notes, which stimulate pecking by other birds. During the sexual tidbitting display of males to females this same call is uttered.

The calls associated with predator avoidance are several, of which the alarm *pit, pit* notes are perhaps most common. With almost any disturbance these metallic-sounding calls are uttered, especially before the birds begin to flee. When actually fleeing on foot they are more likely to utter a series of *chwip, chwip* sounds that are perhaps a variant of the earlier call. The avian predator alarm call is a low, throaty *kurr, kurr, kurr,* which may stimulate freezing or fleeing behavior by other birds. Following such disturbance a soft *put, put* series of notes may be produced, which may prolong the freezing behavior. When held in the hand, adults of both sexes often utter a loud, downslurred *pseu, pseu* note much like those of other New World quails.

Williams reported that prior to copulation or during it females sometimes uttered soft peeping calls, and males usually produced *ut, ut* notes that changed to *wip, wip* sounds during treading. When building her nest, the female uttered a low, repetitive *pa, pa, pa* series of notes, while the male uttered rather different sounds as he handled nesting material.

No special calls other than contact *ut, ut* calls were associated with incubation, and during brooding of young chicks the parents both uttered low *mo, mo, mo* notes when the chicks became scattered. Chicks that are lost utter a loud distress whistle, to which the adults respond with the *cu-ca-cow* call, especially from the male. Adults also uttered the food call when attracting young to a source of food.

In total, Williams found fourteen adult call types in the California quail. Of these, eleven were typical of both sexes, and three characteristic of the male only. Two of the fourteen were associated with social contact, five with alarm responses, six were believed to have reproductive significance (including two agonistic calls), and one was associated with parental behavior. Most of the California quail's calls have their counterparts in the bobwhite. However, Williams related the absence of a call functioning to space winter coveys (as the *koi-lee* is reported to do for the bobwhite) to the fact that winter coveys of the California quail are generally larger than in bobwhites and sometimes tend to come together into very large wintering flocks.

EVOLUTIONARY RELATIONSHIPS

The probable evolutionary history of the California quail has been discussed in the earlier account of the Gambel quail.