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24 Gambel Quail

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Gambel Quail

Callipepla gambelii (Gambel) 1843
(Lophortyx gambelii in *A.O.U. Check-list)*

OTHER VERNACULAR NAMES

ARIZONA quail, Codorniz de Gambel, desert quail, Olanthe quail.

RANGE

From southern Nevada, southern Utah, and western Colorado south to northeastern Baja California, central Sonora, northwestern Chihuahua, and western Texas.

SUBSPECIES (*ex A.O.U. Check-list* and *Check-list of the Birds of Mexico*)

C. g. gambelii: Southwestern Gambel quail. Resident from southern Utah and southern Nevada south to the Colorado and Mojave deserts, northeastern Baja California, and introduced in north central Idaho.

C. g. fulvipectus Nelson: Fulvous-breasted Gambel quail. Resident in north central to southwestern Sonora, and probably north to southeastern Arizona and southwestern New Mexico.

C. g. pembertoni (van Rossem): Tiburon Island Gambel quail. Resident on Tiburon Island, Gulf of California.

C. g. sana (Mearns): Colorado Gambel quail. Resident in western Colorado in the drainage areas of the Uncompahgre, Gunnison, and Rio Grande rivers.

C. g. ignoscens (Friedmann): Texas Gambel quail. Resident of desert areas in southern New Mexico and extreme western Texas.

C. g. stephensi (Phillips): Recently described (1959). Resident in Sonora, near the Sinaloa border (not yet verified).

C. g. friedmanni (Moore): Sinaloa Gambel quail. Resident in coastal Sinaloa from Río Fuerte south to Río Culiacán.

MEASUREMENTS

Folded wing: Adults, both sexes, 105–22 mm (males average 2 mm longer than females).

Tail: Adults, both sexes, 83–107 mm (males average 5 mm longer than females).

IDENTIFICATION

Adults, 9.5–11 inches long. The sexes are different in appearance. This southwestern quail has a blackish, forward-tilting and teardrop-shaped crest as in the California quail but completely lacks the scaly patterning of the underparts typical of the latter. Only on the back of the neck of males is some scaly patterning evident, but this is ill-defined. Male Gambel quail also have a black forehead and reddish-brown crown coloration, and both sexes have more rufescent brown flank coloration than occurs in the California quail. Otherwise the birds are generally grayish brown to brown on the upperparts and tail and have buffy underparts that may be streaked with brown (females) or have an extensive black area on the abdomen (males). Males also have the characteristic black throat pattern that is lacking in females.

FIELD MARKS

Generally limited to desert regions of the southwest, Gambel quail can be identified in the field by the combination of "teardrop" crests and unscaled underparts. The rich reddish-brown flanks of both sexes are visible at considerable distances, and at close range the reddish crown color of males and the black mottling of their underparts may be evident. This species' calls are similar to those of the California quail, but are less metallic and more nasal. The distinctive location call consists of occasionally repeated

chi-ca-go-go notes (occasionally California quail will also add a fourth syllable to their location call).

AGE AND SEX CRITERIA

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

Immatures have mostly buff-tipped greater upper primary coverts which are carried for the first year (Leopold, 1939). The outer two primaries may be somewhat more pointed and frayed than the inner ones in immature birds.

Juveniles resemble females but have dull brown crests and broad bands of pale cinnamon buff above the eyes. They are very similar to California quail of this age except that the nape feathers lack dusky borders and are uniformly gray with more distinct shaft-streaks (Dwight, 1900).

Downy young (illustrated in color plate 110) of this species cannot be easily distinguished from California quail of the same age, but are perhaps in general slightly paler and less yellowish in tone overall. The pale spinal stripe is somewhat tinged with darker streaks in the Gambel quail, while in the California quail it is a slightly brighter buff. Furthermore, the downy California quail generally has less sepia brown (that is, more buff) coloration on the forewing than do the Gambel and scaled quails.

DISTRIBUTION AND HABITAT

A detailed analysis of the range and habitat of the Gambel quail has been made by Gullion (1960), from which the accompanying range map is largely derived. No major changes in ranges have occurred since that time, and his review of the species' distribution by states cannot be improved upon. He found that the species is found in three major climatic and habitat types. One of these is the mesquite (*Prosopsis*), saltbush (*Atriplex*), tamarisk (*Tamarix*), and desert thorn (*Lycium*) shrub associations of desert valleys from Texas west to southern California, Nevada, Utah, and northern Mexico. These areas have similar altitudinal ranges, low annual precipitation totals, and mild winter temperatures.

Especially in the western part of the species' range, it also occurs in upland desert habitats, particularly where a fairly uniform desert vegetation is dominated by cat's-claw (*Acacia*), creosote bush (*Larrea*), desert thorn, skunkbush (*Rhus*), yuccas (*Yucca*), burroweed (*Franseria*), and prickly pear (*Opuntia*). This habitat type occurs on the Mohave desert areas of Arizona, California, and Nevada and to a reduced extent in southwestern

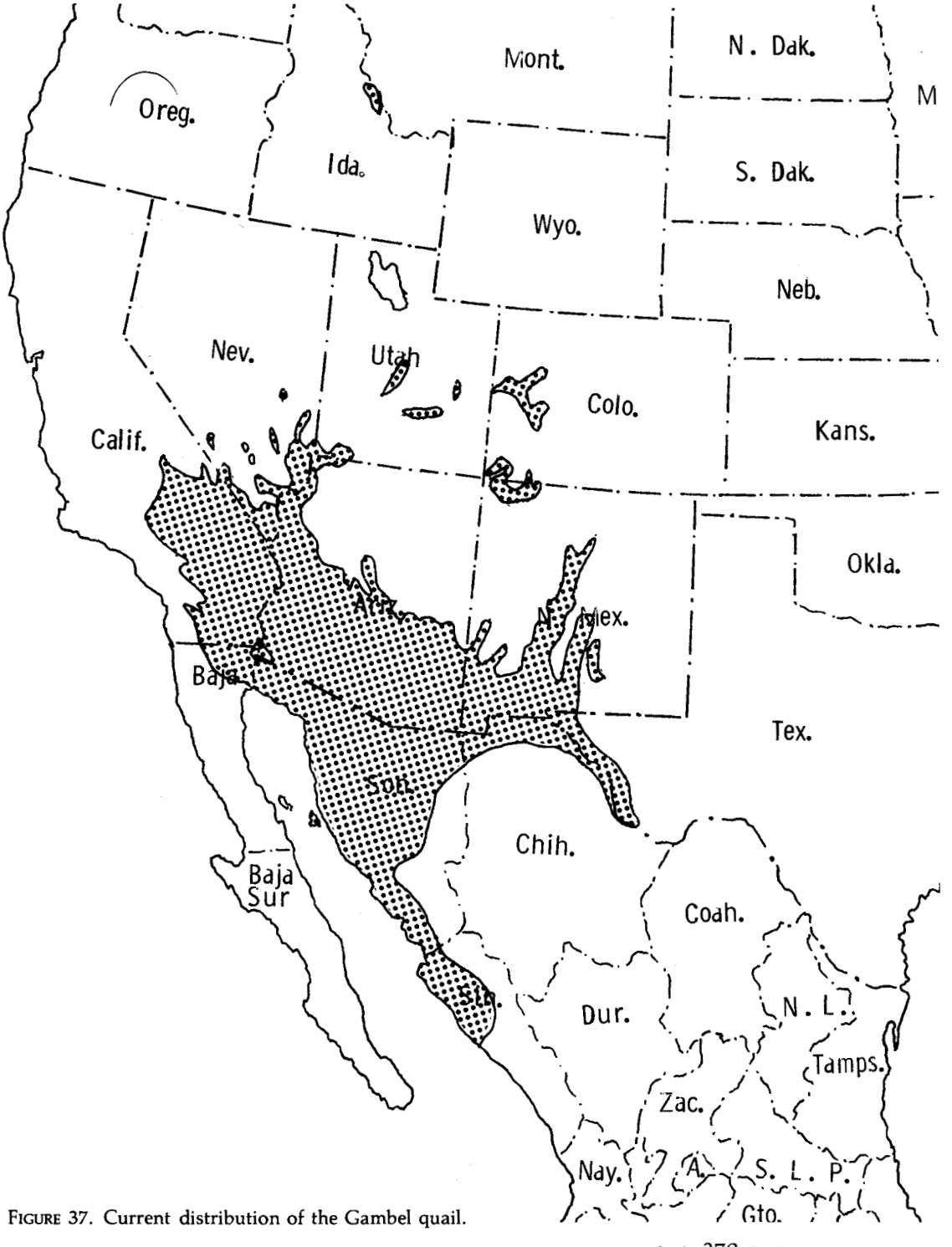

FIGURE 37. Current distribution of the Gambel quail.

New Mexico and Utah. The altitudinal range is from three thousand to forty-five hundred feet, and winter temperatures average considerably above freezing. Although precipitation averages more than in the valley habitats, it is still only from about 3 to 9½ inches. These birds exhibit greater population fluctuations than is typical of lowland habitats, depending on annual productivity. Winter precipitation variation is one of the most important factors regulating these population changes.

In addition to these two warm desert habitats, the species also occurs in the Colorado River basin areas of New Mexico, Colorado, and Utah and as an isolated population in Idaho, all of which are subjected to considerably colder temperatures. The vegetation here is essentially that of the Great Basin desert, with such shrubs as greasewood (*Sarcobatus*), rabbit brush (*Chrysothamnus*), skunkbush, saltbush, and sagebrush (*Artemisia*) being almost universally present. These habitats and climates are marginal for the Gambel quail, and at least in some areas the presence of food in the form of agricultural crops such as alfalfa may be critical for survival. Gullion also suggested that such populations are marginal where snowfall exceeds twenty inches or where at least an inch of snow is on the ground for more than about forty days a year. Where the northern population survives best, the winter precipitation totals are normally quite low, usually well below 50 percent of the total annual precipitation.

POPULATION DENSITY

Breeding populations of the Gambel quail have not been intensively studied as to population densities. Hensley (1954), in studying the birds of desert habitats in Arizona, estimated that the average number of breeding quail pairs per 100 acres on 210 acres of study areas was six, or one pair per 16.6 acres. However, based on one study area of 70 acres, he had an estimated maximum population of twelve pairs per 100 acres, or one pair per 8 acres.

In a study of the breeding bird population of a cholla cactus (*Opuntia*), palo verde (*Cercidium*), and saguaro (*Cereus*) desert community in Arizona, an estimate of 20 territorial male quail per 100 acres has been made (*Audubon Field Notes*, 19:610–611, 1965), or presumably one pair per 5 acres. Also, Hensley (1954) reported that four pairs of Gambel quail occupied a mountain canyon study area measuring twenty-five by eight hundred yards (4.1 acres), suggesting that under favorable conditions a population density of at least one bird per acre may sometimes occur. Gullion (1962) reported that an estimated total of 472 quail were present on a 777-acre

study area in Nevada, or 1.6 acres per bird. This total apparently referred to a late winter population.

HABITAT REQUIREMENTS

Gullion (1960) has suggested several biotic and physical environmental features that may represent limiting factors for Gambel quail. Soils having good populations are residual soils of decomposed granite in the uplands of Nevada; such soils support a relatively luxuriant and diversified vegetation. Transported soils of river bottoms also support luxuriant shrub growth and high quail populations. Populations are also highest where January temperatures do not drop below forty degrees F., and, as mentioned earlier, winter snow cover is probably an important limiting factor in northern marginal populations. However, the Colorado race of Gambel quail is known to survive winter temperatures as low as eight degrees below zero in New Mexico, the Texas race of Gambel quail occurs in areas having minimum winter temperatures of five degrees below zero, and in Utah and Idaho the introduced race *gambelii* have survived temperatures of approximately forty degrees below zero.

Although lowland populations of Gambel quail depend on subsurface moisture that may originate several hundred miles away, upland populations evidently require a winter precipitation of more than five inches (Gullion, 1960). This of course is not a reflection of drinking water needs but of the effects of the precipitation on vegetational growth. Swank and Gallizioli (1954) considered December to April in Arizona to be the most critical months for precipitation, and Gullion (1960) correlated quail populations with the precipitation totals of the preceding October to March. Apparently winter germination and growth of green plants is vital to the breeding success of this species, possibly because of its effect on vitamin A storage in potential breeding birds (Hungerford, 1964). Raitt and Ohmart (1968) reported that in New Mexico the fall productivity index based on age ratios was closely correlated with amounts of precipitation during the preceding May and June rather than those of the previous fall, winter, or early spring, indicating a lack of strict dependency on such winter rainfall. They suggested that the effects of irrigation or a winter climate that permits an accumulation of soil moisture might account for this apparent difference in climatic correlation.

The importance of free water for drinking purposes by Gambel quail is not completely clear. Gullion (1960) believed that where a combination of high humidity and fleshy plants occurs, the birds can live an entire lifetime without drinking water. Hungerford (1960) concluded that water catch-

ments were nonessential in southern Arizona, where moist succulent plant foods are normally available. However, on desert uplands, such as in Nevada, there may be a critical period for moisture from about mid-June to mid-July, when succulent spring annuals have dried up and summer thunderstorms have not yet occurred. During such times, if succulent plants are not available, artificial watering structures may be quite important to the species (Gullion, 1960). Miller and Stebbins (1964) report that in Joshua Tree National Monument the Gambel quail occurs primarily in the vicinity of springs, and the greatest distance from water which they have recorded for this species was one and a half miles at a time when succulent vegetation was widespread. Most coveys probably stay within a mile of water when it is needed.

Nesting cover requirements for the Gambel quail are simple, consisting of desert shrubs or trees, with the primary requirement apparently being a source of shade from the midday sun (Bent, 1932). Brooding requirements no doubt include brushy escape cover, shade for resting, and foraging sites where insects and small green plant growth is readily available. Grit sources and dusting locations are readily available in desert habitats.

FOOD AND FORAGING BEHAVIOR

In common with the California quail, the Gambel quail relies very little on animal sources of food, adults taking perhaps as little as 0.5 percent of their annual food from this source (Judd, 1905a), with a maximum usage of 12 or 13 percent during spring and summer (Martin et al., 1951). Otherwise, the birds rely predominantly on the foliage and seeds of a large array of plants.

Judd's analysis (1905a) of twenty-eight food samples from Arizona and Utah indicated that virtually no fruit material is consumed and only a very small amount of cultivated grains (3.9 percent of annual total). Rather, leafy materials, mainly legumes, and seeds of a variety of species made up over 95 percent of the total sample, with these two food categories totaling 31.9 and 63.7 percent by volume, respectively. Legume seeds alone made up 21.2 percent of the total food material, especially of those of alfalfa and bur clover (*Medicago* spp.). Gullion (1960, 1966) noted that at least ninety-one species of plants are consumed by Gambel quail in southern Nevada, but the availability of species representing only three groups, namely deervetch (*Lotus* spp.), filaree (*Erodium*), and a few herbaceous legumes (*Astragalus* and *Lupinus*) determines the abundance of Gambel quail in this area.

Hungerford (1962) examined the seasonal variations in food consumed by Gambel quail in southeastern Arizona, based on the study of 221 samples. He found that various legumes (*Lotus, Lupinus, Mimosa, Prosopsis*) were the most important food sources, with their leaves, flowers, and seeds all being consumed. Filaree seeds and flowers were a highly preferred food source as well. On a yearly basis, seeds made up 60.7 percent of the diet and were important foods throughout the year. Considering only life-form of food sources, forbs were most important, making up 54.2 percent of the annual diet, shrubs were second, totaling 31.8 percent, and grasses, animal foods, and unknown plants made up the remaining amount. During spring, a high 1:1 ratio of succulent to nonsucculent plants was present, while during fall and winter this ratio dropped to about 1:2. Apparently these succulent food sources, during dry periods or in areas where free water is not normally available, provide important sources of moisture and are highly important aspects of the quail's ecology.

A study by Campbell (1957) on the fall foods of the Gambel quail in New Mexico provides an additional index of the diverse food usage of this species. Of fifty-seven crops studied, all had seeds and/or fruits present, and collectively eighty-seven plant species representing twenty-seven different families were present in the crops. However, foods representing twenty-two species of plants accounted for more than 90 percent of the sample volume, including five species of legumes, four composites, four grasses, and three chenopods. Campbell concluded that the Gambel quail's flexibility in foraging behavior in utilizing so many different food sources helped to explain its success in agricultural areas, where the vegetational complex is quite different from that prevailing in undisturbed desert habitats.

MOBILITY AND MOVEMENTS

The movements and social organization of Gambel quail coveys has been studied by Gullion (1962) in Nevada, on a 777-acre area of thorn shrub vegetation. A total of twenty-four coveys were present on the area, ranging from 3 to 40 birds and averaging 12.5. An estimated total of 472 birds were present, of which 217 banded birds were used to establish covey organization and movements. There were three major areas of use on the study area, with some overlapping of home ranges. The home ranges of ten coveys varied from 19 to 95 acres, averaging about 35.7 acres per covey. No clear correlation occurred between covey size and size of home range, with the largest covey (22 birds) having a 95-acre range, the second largest (21 birds), a 37-acre range, and a still smaller covey had an intermediate range.

During the winter, covey movements appeared to be erratic. From late

December to the following April, the ten coveys ranged over areas with diameters of from 1,500 to 4,200 feet, averaging 2,340 feet. One covey of twenty-two birds consisted of at least four subgroups and moved about over a sixty-three-acre area, then all moved into a new area 2,200 feet away. After staying in the new area for at least ten days, the covey disappeared from the study area, with a few of the birds eventually returning to the location where they were originally trapped.

Seasonal variations in covey movements were considerable and were influenced by the age composition of the coveys, with coveys composed of adults moving considerably farther than did brood coveys. During the winter period of December through late January, five adult coveys moved an average of 103 feet per day, while thirteen brood coveys averaged 63 feet per day. The movements increased in late January and early February, with average daily movements of 264 feet for adults and 131 feet for broods. During late March and early April there was a considerable prenesting shuffle, with coveys actively moving about, and the five adult coveys averaged 1,029 feet per day during this time. However, after about the first week of April, most of the coveys became sedentary, with the exception of a few new arrivals on the study area.

Individual movements of three birds during periods between late morning and midafternoon ranged from 400 to 1,250 feet, while the movements of forty-two banded birds over twenty-four-hour periods averaged 755 feet but were as much as 2,800 feet. One male moved at least 2,400 feet in a forty-eight-hour period and another male at least 3,800 feet in ninety-six hours. Another male moved 4.7 miles between April and November, while a fourth male moved 5 or 6 miles between late April and October. The longest recorded movement was of an adult female, which moved 6.5 miles from its banding site in somewhat over two years, and was at least four and one-half years old when it was killed.

No definite fall dispersal pattern for single quail could be established, but a spring dispersal pattern was clearly evident. This dispersal, which consisted of covey-shifting, was performed mostly by young males, plus a few young females. Although the evidence was not clear, major dispersals over long distances probably involved entire coveys rather than individual birds.

SOCIAL AND REPRODUCTIVE BEHAVIOR

Gullion's (1962) study indicated that coveys of Gambel quail consist basically of family units of 5 to 7 birds or their aggregates (9 to 13; 17 to 22). Winter coveys might consist either of such combined broods or of vary-

ing numbers of nonbreeder adults. Although some overlapping of home ranges of coveys does occur, there is considerable covey fidelity, with little of the covey exchange that has been reported for other species of quail. Such covey exchange that Gullion found (20 of 217 birds) occurred mostly during the prenesting shuffle, with only 5 birds shifting during the earlier winter period.

The study by Raitt and Ohmart (1966) in southern New Mexico provides one of the best analyses of seasonal variations in social behavior that is available for the Gambel quail. During late winter, pair formation and increased hostility among males begins to cause the dissolution of coveys, which in New Mexico begins in March. The process of pair formation is a subtle one, which apparently occurs over a prolonged period of contact. Raitt and Ohmart thought that chases of females by males, during which they uttered explosive high-pitched notes together with longer and lower-pitched, softer notes, might be associated with pair formation under natural conditions. Such chases rarely if ever occur in captive birds which have been held in pairs through the prebreeding period, but if a female is introduced to a lone male in breeding condition strong chases of this type will immediately occur, and care must be taken that the female is not killed by the male. Thus, it would seem that initial male-to-female responses are not greatly different from male-to-male behavior, except that the female attempts to escape and performs submissive responses such as huddling that usually serve to break off attacks by the male. I have not seen strong wing-drooping during such display in the Gambel quail, but evidently it does occur. Gorsuch (1934) described such an encounter as follows:

"One day, while observing a whistling cock that was known to have used the same bush from which to call for over three weeks, a clucking sound was heard from down the wash and shortly a hen appeared. Immediately the cock sighted her his notes became fewer and shorter, and when she was within thirty feet of his perch he became greatly excited, jumping about the bush as if much disturbed, and talking to her meanwhile in a variety of notes. When she approached to within fifteen feet he . . . leaped to the ground and slowly but eagerly advanced to her. After walking around the hen in short circles several times, expanding his chest and trailing his wings in display they engaged in low-voiced conversation and wandered slowly away; it was definitely known that no nest existed within 200 yards of this whistler's post."

When males are chasing males, fighting may occur; this should not be regarded as territorial defense but only as a means of establishment of social dominance. Such attacks consist of rapid pecking movements and short vertical flights as each bird tries to get above the other bird and peck its

skull. After a few such attacks, one bird usually makes a quick retreat and in a small cage may be caught by the dominant bird, whereupon its back, nape, and skull may be seriously damaged by pecking.

As the coveys are breaking up and strong pair bonds are forming, *cow* calling by unmated males begins. In New Mexico this may occur as early as mid-March, but reaches a high level in April and May, declining in June and terminating completely in late July or early August. Its duration thus does not conform to the period of pair formation, and a census of calling males should obviously not be regarded as a census of pairs in the area. Rather, its cycle generally follows the testis activity cycle, and it is thus a reflection of male sexual tendencies of unpaired birds. Probably no *cow* calling occurs in mated males, according to Raitt and Ohmart, and the study of Ellis and Stokes (1966) confirmed this opinion. These authors indicate that the call, which they refer to as the *kaa*-call, is usually given from an exposed perch and has a function analogous to the advertising song of passerine species. During the call, the male stands in an erect posture, with his abdominal patch wholly visible and the crest held vertically erect.

Gambel quail are strongly monogamous. The gonadal activity cycle of the female lags about two weeks behind that of the male, and in New Mexico laying begins in late April. Gorsuch (1934) indicated that a depressed area about one and one-half inches deep and five to seven inches in diameter is scratched out and variably lined. The first egg is deposited shortly, and the remaining eggs are deposited daily thereafter, with lags of one to three hours on each succeeding day. After four to six eggs, a day is skipped, and the cycle begins again. After about three such cycles of four to six eggs, the clutch is complete. Gorsuch found clutches of up to nineteen eggs at forty-four nest sites, but twenty-nine of the nests had from ten to sixteen eggs present; thus, twelve to fourteen must be regarded as a typical clutch.

Incubation is performed by the female alone, with the male usually sitting at a perch some forty to eighty feet away. When the nest is approached by an intruder, the male typically performs a "broken wing" distraction display (Gorsuch, 1934). Incubation usually requires from twenty-one to twenty-three days, with pipping usually occurring on the twenty-third day. Gorsuch estimated that about ten days might be needed for nest selection and construction, thirty-eight to forty-two days for egg-laying and incubation, and nearly three months is required for raising the brood to an independent state. Thus two broods cannot be raised successively by a single pair even with the long nesting season typical of the southwestern desert. However, during highly favorable nesting seasons supplementary nestings may be achieved by two different methods. The males may take over the care of the brood, leaving the female free to begin a second clutch, or, more

commonly, the chicks may be "weaned" when about a month old and left in the care of older birds of the area, thus allowing the pair to start a second clutch (Gullion, 1956a). In one desert area where such double-brooding occurred, the average number of chicks per adult pair was fifteen, whereas on the valley habitats where double-brooding did not occur the average number of chicks per adult pair was ten.

When the young are hatched, the family leaves the nest-site and does not return again. Brooding by the female occurs on shady and well-sheltered areas, while the male typically "stands guard." As the brood moves, the male usually takes the lead, with the chicks following and the hen bringing up the rear. Males leading young chicks regularly perform distraction displays, while the hen and young "freeze," or both adults may fly off as the young remain in place (Gorsuch, 1934). Like all young galliforms, the chicks feed almost exclusively on insect life during the earliest part of their life but soon begin to take leaves and other succulent vegetation and within a few months are consuming about 90 percent vegetable materials (Gorsuch, 1934).

Vocal Signals

The most complete analysis of vocalizations of the Gambel quail is that of Ellis and Stokes (1966), which will be followed here. They grouped the species'calls into those associated with group activity, with feeding relationships, with responses to enemies, and with agonistic and sexual phases of reproductive behavior.

Calls important in integrating covey activity are the basic contact *took!* note, a conversational *ut*-growl, and the location call. The contact note is uttered by both sexes and carries only a short distance. It occurs at all times of the day, but is especially associated with foraging. A similar call, the *ut*-growl, is the same note with an added trill and is especially prevalent when the birds find food or water after being deprived of them.

The location or separation call is a four-noted *ka-KAA-ka-ka* (also interpreted as *cow-COW-cow-cow* or *chi-CA-go-go*) and is produced by birds when separated from their mate or the covey. Both sexes produce the same call, but sufficient individual variation occurs in the call (which is the most acoustically complex as to cadence and amplitude characteristics) that individual recognition is typical. Visually isolated birds keep in contact by use of this call, and males can distinguish the location call of their mates from those of other females.

No specific food calls were noted by Ellis and Stokes, nor have I heard any. Evidently paired males do show or pick up food particles in front of their females, a display ("tidbitting") that is widespread in galliform birds,

but Ellis and Stokes did not notice any associated calling. However, Prososki (1970) did hear calling in this situation.

Several calls are associated with responses to enemies. The most typical alarm note of Gambel quail, as well as other *Callipepla* species, is a repeated *chip-chip-chip* as the birds investigate any disturbance during moderate alarm or curiosity. When thoroughly frightened and rushing for cover, a bird utters a raucous *squawk* followed by a series of *chip* notes, or the two kinds of calls may be alternated. The *squawk* note is both louder and more prolonged than the *chip* sounds, but they probably intergrade with one another. During times when the birds are being held in one's hand, they usually utter loud, down-slurred distress *kee-OW*! notes, repeated almost indefinitely at intervals of about one-half second. Both sexes use the call, but individuals vary in the ease with which the call can be elicited from them.

The reproductive phase of sexual behavior has several associated calls. One of the most important of these is the *kaa* or *cow* call, already discussed in the section on social and reproductive behavior. Another is the location or separation call, *ka-KAA-ka-ka*, uttered by members of a pair whenever they are visually separated. Ellis and Stokes noted that during copulation at least the female, and probably also the male, uttered a series of short squealing calls. When an unpaired male is displaying toward a female, he faces her and utters a series of *wit-WUT* aggressive notes that are the same as occur when two males are threatening one another. At this time the head is bobbed somewhat, causing the erect plumes to vibrate, and the bird stands in an erect posture.

During aggressive encounters between two males, the same *wit-WUT* call is uttered, often alternated with pecking movements or actual attacks. In such situations the calling may be almost continuous as the birds face one another, seemingly unwilling to attack or retreat. After a varying number of such threats and attacks, one of the birds typically utters a cat-like *meah* call, at the same time lifting his beak almost to a vertical position. This call no doubt is homologous to the *squill* of the California quail but is both more prolonged and much slower in the associated head movements. This call usually stimulates the other male to respond in the same fashion and generally leads to a termination of the encounter.

Observations on the vocalizations of a male hybrid bobwhite × Gambel quail (Prososki, 1970) allows for the establishment of some probable vocalization homologies between these genera. The announcement call of the unpaired male bobwhite is a whistled *bob-white!* (Stokes, 1967). The hybrid's call was a similar two-note call, but the two notes were virtually identical in volume and frequency characteristics, sounding something like *cow-COW!*

The separation call of the male hybrid was apparently the same call as the male's announcement call, whereas in the bobwhite two calls (*hoy-poo* and *hoy*) serve this purpose. The calls are also used in agonistic situations by male bobwhites.

Two calls were produced in agonistic situations by the hybrid male, a two-noted *porquoi* and a growling *ker-ra-wa* call. Typically he would begin with a number of *ker-ra-wa* calls, followed by several *porquoi* notes. The *ker-ra-wa* calls sonagraphically most resemble the *hoy-poo* calls of the bobwhite, while the second note of the *porquoi* approached the *meah* in its acoustic characteristics. No sounds resembling the Gambel quail's *wit-WUT* call were produced.

The hybrids also produced chipping alarm calls, hand-held distress calls, contact calls, tidbitting calls, and copulation calls, all of which were comparable to those of both parental species, since interspecific differences are generally not great in these calls.

It is of interest that in this group of quails the male call that is used to announce the location of unmated males (thus also communicating information on species, sex, and reproductive state) is a simple, one-syllable note in at least three species (Gambel, scaled, and California quails). However, the call used by both sexes to announce the location of a bird separated from its mate and serving both for individual recognition and for homing purposes consists of two notes (in elegant and scaled quail), three (in California quail) or four (in Gambel quail), varying in cadence, pitch, and loudness but all having similar harmonic characteristics. In the Gambel and California quails the male announcement call is, in effect, a single note "excerpt" from the longer location call, while in the scaled quail the male's announcement note more closely approaches a pure whistle. This distinction between a harmonic-rich location call and a nearly harmonic-free whistle for a male announcement call is even greater in the bobwhite. The bobwhite also seemingly has a greater number of agonistic calls than do the species of *Callipepla*, and in general its acoustic communication system appears to be more complex.

The Gambel quail apparently has two basic male agonistic calls, one of which (the *wit-WUT*) is used during sexual display toward females and aggressive encounters with other males, and the other (the *meah*) which is used only toward other males and apparently serves to break off aggressive encounters. Similarly the California quail has two calls, the *wip-wip*, which serves the same function as the Gambel's *wit-WUT*, and the *squill*, which occurs during high-intensity male-to-male threat. In contrast, the scaled quail seems to lack a call comparable to the *wip-wip* or *wit-WUT*, and the head-throw call is performed by both sexes in agonistic situations,

although it is used predominantly by males. Again, the bobwhite is the most complex in its agonistic vocabulary. Both sexes use the *hoy* and *hoy-poo* calls in agonistic situations, and two additional calls, the *squee* and "caterwaul," are largely but not entirely characteristic of the males (Stokes, 1967). The *hoy, hoy-poo,* and "caterwaul" calls seem to represent one intergrading motivational complex, while the *squee* call has a different seasonal and contextual occurrence. Thus a certain vocal duality is present, but it is difficult to judge possible homologies in these calls. One might only imagine that the evolutionary trend has been from a situation (as in the scaled quail) where both sexes perform a common call in an agonistic situation to one (as in Gambel and California quail) where the male has separate vocal signals for male-to-male situations and male-to-female situations, and finally (as in bobwhite), to a condition where both sexes have a complex intergrading series of calls associated with varying agonistic situations.

Ellis and Stokes (1966) list a total of ten call-types for the Gambel quail, of which at least seven are common to both sexes, two occur only in males, and one (the copulation call) occurs in the female and possibly also the male. Stokes's analysis (1967) of the bobwhite's vocalizations indicated a considerably larger number of vocalizations, but the intergrading qualities of many of the calls make a strict numerical comparison impossible.

EVOLUTIONARY RELATIONSHIPS

The close similarities in downy and adult plumage patterns, as well as strong behavioral similarities, clearly indicate that the Gambel and California quail are close relatives. The ecological differences between the two species prevent extensive sympatry, but where limited contact does occur hybridization has been found (Miller and Stebbins, 1964). It would seem reasonable that the Sierra Nevada range might have provided an effective geographic barrier that allowed speciation to develop to the point that now exists and has still virtually prevented any extensive population overlap, partly because of the major climatic differences prevailing on the two slopes of this range. It also seems possible to assume that the common ancestral type may have had a range in the southern part of the continent similar to that now occupied by the Gambel quail, and that as the ancestral California quail adapted to the moderate climate of interior California it gradually extended its range northward into the coastal portions of the Pacific northwest.