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Quail Music*

The complex calls of a bird contain clues to its evolution

by Paul A. Johnsgard

The danger implied by an owl's hooting, the peace suggested by a dove's cooing, and the good cheer represented by a robin's song are all traditional, universal interpretations of bird vocalizations that have nothing whatever to do with the actual biological functions of these utterances. Only by field or laboratory investigations is it possible to gather information about the purpose of bird calls and songs. Some are territorial proclamations or mating invitations; others serve as warnings or threats, help synchronize group movements, increase the probabilities of efficient reproduction, and improve the chances for survival.

Ethological research has revealed that these vocal communications are highly specialized behavioral adaptations that can shed light on evolutionary processes that have affected whole groups of birds. The calls of the quails of the New World are a good example.

This group of birds includes some thirty species, about half of which are limited to the tropical forests of Central and northern South America. The other species are North American, ranging as far north as southern Canada. Morphological evidence favors the view that the most generalized, or "primitive," of these species are the tree quails of Mexico's moist mountain forests. The more open-country and arid-adapted species, which extend into the United States, are anatomically more specialized, or "advanced," and probably were derived from forest-adapted ancestral stock somewhat like the modern tree quails.

The vocal requirements for all quail species are similar, reflecting basic similarities in their breeding biology. Effective communication between the adults and young is needed to provide maximum efficiency for protecting and rearing brood. Calls that facilitate the maintenance and regrouping of pairs, families, or coveys are also needed, since the birds depend on social banding as a defense against predators. The effectiveness of alarm, or warning, signals in reducing individual mortality has no doubt been an important factor in evolution of covey-forming behavior. Calls that achieve a means of individual recognition between members of a pair also facilitate monogamous pair bonds. Finally, calls serving to announce the location of unmated but sexually active males are also required.

A species with a minimum vocal repertoire is the scaled quail (*Callipepla squamata*). This desert and grassland bird extends from Texas and New Mexico southward through the arid Mexican uplands to the Valley of Mexico. It has a bushy, whitish crest, larger and paler in males than in females, which is the basis for its vernacular name "cottontop quail." In the winter, the bird lives in coveys of from 15 to 150 birds and ranges over areas of from 50 to about 350 acres.

The scaled quail's repertoire consists of an unmated male announcement call, "whock"; a separation call, "pey-cos," used by individuals of both sexes when isolated from their mates or coveys; an aggressive "head-throw" call, which is primarily uttered by a male when another male approaches his mate too closely; a general alarm note, "chip"; an avian predator alarm call,

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"oom-oom-oom"; and a distress call, "ciew." There are probably other calls present such as soft contact notes and specialized parental calls.

This adult repertoire develops during the individual's growth. Newly hatched quails typically produce "peeping" notes when they are separated from their parents; this vocalization gradually changes to the adult separation call. Chicks also have loud distress calls, which increase in volume and frequency range as the birds mature. Their softer contact notes probably keep the brood and parents in proximity to each other and persist in adults as calls having comparable functions. The alarm calls gradually appear at various ages after hatching; and the exact time of their initial appearance is probably dependent on specific evoking stimuli.

The bobwhite (*Colinus virginianus*) is a quail associated with forest edge and brush habitats. The male bobwhite lacks a crest, and in contrast to the scaled quail, the sexes are markedly different in plumage, their winter coveys average about ten to fifteen birds, and their home ranges are about ten to fifty acres. The smaller home range of bobwhites is a probable reflection of the greater availability of food, while in the colder parts of their range the smaller covey size reflects the optimum number of birds required to form an efficient heat-conserving ring of birds during nocturnal roosting.

The bobwhite also has a greater diversity of vocalizations than the scaled quail. In addition to the calls typical of the scaled quail, the bobwhite has at least two contact calls, a food-finding call (typically used by females to call the young to a food source), and a female copulation call. Also, two distinctly different calls are associated with male-to-male aggression and indicate differing degrees of social dominance.

The bobwhite's separation notes also exhibit greater variation than the scaled quail's, including an increasingly louder series of "hoy," "hoy-poo," "koi-lee," and "hoyee" sounds that serve not only to reunite separated pairs but probably also to space coveys, attract males to unmated females, and repel intruders. Studies by ethologist Allen Stokes indicate that several additional calls are produced by adults brooding young, including two different alarm notes, a "broody" call, and a "take-cover" call. This surprisingly rich vocal repertoire—twenty-four different calls—is greater than that reported for nearly all bird species.

The acoustic differences between the scaled quail and the bobwhite are worthy of note. The basic adult separation notes of the two species ("pey-cos" and "hoy-poo") are somewhat comparable in their cadence, frequency, and harmonic characteristics, but sufficient differences are present to provide for species-specificity. Furthermore, the unmated male calls ("whock" and "bob-white") differ in number of syllables and frequency; and whereas the bobwhite utters a nearly pure whistle, harmonic over tones in the scaled quail's whock call produce a nasal sound.

Similar comparisons may be made with other quail species. Calls of unmated males typically exhibit marked species-specificity but show little variation among individuals, while separation calls generally exhibit sufficient individual diversity and harmonic complexity to facilitate individual recognition by mates. Distress and alarm calls are often nearly identical even among rather distantly related species. Although the typical quail distress call is loud and piercing, with a broad frequency range and resultant ease of localization, the alarm call is a series of soft "pit" or "ick" notes that carry only a short distance and are of brief duration. Distress calls tend to attract other quails and may result in attempted assistance (males may threaten or peck at a predator attacking another quail); alarm calls cause general retreat and stimulate others to utter the same notes.



The bearded tree quail is found in the mountainous cloud forest of east-central Mexico (smaller area). Gambel's quails occupy mesquite, saltbush, and thorn shrub habitats in desert valleys throughout northern Mexico and the American Southwest (larger area).

Distribution of the Bearded Tree Quail and Gambel's Quail



The scaled quail's range centers on the Chihuahuan desert, stretching up into the Southwest. It thrives best where there a combination of annual weeds, shrubby ground cover, and available surface water.

Distribution of the Scaled Quail



With the largest range of all quail species, the bobwhite can be found from southern Maine through the Midwest to the Mexico-Guatemala border. Bobwhites prefer woody or brushy river valleys.

Distribution of the Bobwhite (*Colinus virginianus*)

If the bobwhite evolved a more diversified and complex vocal repertoire in conjunction with its close ecological ties to heavy brush and forest-edge habitat—and its associated, reduced usefulness for visual signals—it stands to reason that forest-dwelling quails should have the most complex vocal signals of all the New World quails. Current evidence tends to favor this view. Compared with open-country species, forest-adapted quails are generally large and rather inconspicuously patterned, with heavy bills and stout feet. They consume insects, berries, seeds, and other materials uncovered by scratching in the forest litter or under the soil surface. They move about in small groups (probably made up of individual families), lack elaborate rests or strong sexual differences in appearance, and are far more often heard than seen by humans.

Some of the earliest observations on the vocal behavior of these forest-dwelling quail species were made by mammalogist H. E. Anthony on the appropriately named singing quail (*Dactylortyx thorucicus*). Observing two adult birds kept in separate cages on different sides of a house, he learned that the birds would not sing when they were in view of each other, but did sing each morning if they could not *see* one another. One bird would utter a series of invitational notes, which was immediately followed by a much more complex melodious series of notes by the other. The duetting continued for some time, with the birds finally stopping in unison.

Until recently, there was no suggestion that the tree quails, anatomically the most generalized of the living species of quails, produced comparably complex duets, although it was known that these species commonly uttered dawn and dusk choruses. Previous observers universally have attributed such choruses only to males, a view that has seemed improbable to some on the basis of the known duetting by related species. Thus, while doing field work in eastern Mexico, I was particularly pleased to locate and place in cages five bearded tree quails (*Dendrortyx bar-*

batus): two pairs and an extra female. After adjusting for a time to their new surroundings, the birds began to perform their dawn choruses. The entire group typically sang in unison for fifteen to twenty minutes at about sunrise. Presumably these dawn and dusk singing periods serve to announce the locations of pairs or families to other quails in the area and directly or indirectly may facilitate optimum population distribution. When together, members of the group almost constantly chattered in low, guttural sounds, interspersed with a variety of soft whistles, rattles, and other vocal signals, which are undoubtedly of great importance in maintaining contact with mates or family members in densely vegetated habitats.

These examples of the vocalizations of representative quail types suggest that the forest-dwelling quails are more complex in this respect than are their open-country relatives. Since zoogeographic and morphological evidence favors the view that the open-country species were derived from forest-dwelling forms rather than vice versa, it seems that the evolutionary pattern in the quail group has been toward decreased complexity and diversity of vocalizations as increasingly arid and more open habitats have been colonized. Acoustical signals used for grouping birds at dawn and dusk have been lost, and the complex duetting behavior has been replaced by more generalized separation calls. In the case of males, the separation calls have also been variously modified to serve as species-specific signals for announcing the locations of unmated birds. While uttering such calls, these males often stand in relatively exposed vantage points, maximally exhibiting their distinctive plumages.

The overall size and complexity of a bird's vocal repertoire, or language, is a compound result of its ecological needs for effective vocal signals, its anatomical limitations, and its innate or acquired potential for the use of vocal signal systems. By deciphering the calls of quails, we are coming to learn more about the actual patterns of evolutionary divergence and specialization that these birds have followed.



In preparation for his book, *Grouse and Quails of North America* (University of Nebraska Press, 1973), Paul A. Johnsgard undertook field work in Mexico and the Midwest where he studied the ecology and behavior of various quail species. His research focused on the role of visual and acoustic communication systems and the evolutionary processes that shaped them. A professor of zoology at the University of Nebraska, Johnsgard has written several articles for *Natural History* based on his ornithological studies. "Natural and Unnatural Selection in a Wild Goose" appeared in the December, 1973, issue. [p.2]