30 Harlequin Quail

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Harlequin Quail

Cyrtonyx montezumae (Vigors) 1830

OTHER VERNACULAR NAMES

BLACK quail, Codorniz Encinera, Codorniz Pinta, crazy quail, fool quail, massena quail, Mearns quail, Montezuma quail, painted quail, squat quail.

RANGE

Southwestern United States south to Oaxaca, Mexico. The doubtfully distinct species C. ocellatus (Gould) extends from southern Oaxaca to Nicaragua.

SUBSPECIES (ex Check-list of the Birds of Mexico)

C. m. montezumae: Massena harlequin quail. Resident from Michoacán, Oaxaca, Distrito Federal, Hidalgo, and Puebla to Nuevo León and west central Tamaulipas.

C. m. mearnsi Nelson: Mearns harlequin quail. Resident in western central Texas, central New Mexico, and central Arizona south to northwestern Mexico, including northern Coahuila (Condor 57:162).
C. *m. merriami* Nelson: Merriam harlequin quail. Known only from the eastern slope of Mount Orizaba, Veracruz.

C. *m. sallei* Verreaux: Sallé harlequin quail. Resident from Michoacán south through Guerrero to east central Oaxaca.

C. *m. rowleyi* Phillips. Recently described from Guerrero (1966); not yet verified.

**MEASUREMENTS**

Folded wing: Adults, both sexes, 110–31 mm (males average more than 120 mm, females under 120 mm).

Tail: Adults, both sexes, 47–63 mm (no consistent difference in the sexes).

**IDENTIFICATION**

Adults, 8–9.5 inches long. The sexes are very different in appearance. Males have a beautiful facial pattern of black or bluish black and white and a soft, tan crest that projects backward and downward over the nape. The upperparts of males are grayish to olive brown, extensively spotted and marked with black, white, and buffy markings. The sides and flanks are dark grayish, with numerous rounded spots of white, cinnamon, or rufous brown, depending on the population. The breast is unmarked brown, grading gradually to black on the abdomen and undertail coverts. Females are generally cinnamon-colored, with blackish markings extensive on the back. The female has a small, buffy crest that is less conspicuous than the male’s and a mottled brown and buffy face with a whitish chin and throat. The upper surfaces of the back and wings are extensively mottled, and the underparts are mostly buffy with black flecks or streaks in the abdominal region.

Ocellated quail may be distinguished from the harlequin quail of southern Mexico as follows: southern populations of harlequin quail have the white lateral spotting reduced to their anterior portions, while the posterior flank spots are dark chestnut. Male ocellated quail also have their midbreast and upper abdominal areas a much lighter, generally buffy or slightly tawny color and instead of gray flanks with chestnut spotting have chestnut flanks with black and gray cross-markings. Females have somewhat paler and more pinkish breasts than do female harlequin quail of southern Mexico and differ from the more northerly populations by having buffy rather than white shaft-streaks on the upperparts.

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FIELD MARKS

Males are unmistakable if their distinctively patterned face can be seen or if their extensively spotted flank pattern is visible. Females are more uniformly cinnamon-colored below than are other species of quails. Unlike the scaled quail of the same region (which occurs in more open habitats), harlequin quail will rarely run and instead tend to crouch and hide. They are rarely found far from pine-oak woodlands throughout their entire range. The distinctive call consists of a series of uniformly paced whistling notes, slowly descending in scale. It has not yet been determined whether the ocellated quail has an exactly comparable call, but current evidence would suggest that it does not.

AGE AND SEX CRITERIA

*Females* lack the black and white ornamental patterning of the face and throat of adult males, having instead a white or buffy chin and throat. *Immatures* may be recognized by the upper greater primary coverts (Petrides, 1942; Leopold and McCabe, 1957), which are edged with buffy or barred near the base with buff, whereas in adults they are spotted with whitish (males) or barred with wide white markings. Also in immatures the outer two coverts are pointed rather than rounded. The condition of the outer primaries does not appear to be very useful in determining age. *Juveniles* initially resemble adult females, and young females continue to do so but may be recognized by the transverse barring on the head rather than longitudinal striping as in adults. Juvenile harlequin quail males soon acquire dark underparts and flanks, but whereas adult males have a double row of white spots on a dark background in young males these feathers are pale, with a double row of dark. The head remains juvenile-like for some time (Swarth, 1909).

*Downy young* (illustrated in color plate 110) of the harlequin quail (and presumably also the ocellated quail, which is undescribed) may readily be recognized by the patch of ochraceous buff on the rear of the wings, and the relatively unpatterned back, which varies from argus brown in the middorsal area to a cinnamon buff which forms two incomplete stripes just below the darker middorsal area. The crown is a light chestnut and the rest of the head is pale cinnamon buff, with a narrow dark line extending from the back of the eye to the posterior tip of the crown.

DISTRIBUTION AND HABITAT

The United States distribution of the harlequin quail is limited to parts
of Texas, New Mexico, and Arizona. In Texas it is currently a rare, local resident, mostly west of the Pecos River, although possibly a few still persist on the Edwards Plateau (Peterson, 1960). The bird may formerly have occurred in all the counties west of the Pecos River except El Paso County and eastward through Crockett and Val Verde counties as far as about the ninety-ninth parallel, but by the mid-1940s as a result of overgrazing the bird was found in normal numbers only in the Davis Mountains and parts of the Big Bend (Principal game birds and mammals of Texas, 1945).

In New Mexico the species was once fairly common in the southwestern part of the state, especially near the headwaters of the Gila, San Francisco, and Mimbres rivers (Bailey, 1928). Now its range is greatly restricted, and it occurs only where rank grasses still grow, particularly near the summits of mountains in the Capitan, Sacramento, San Mateo, Black, and Mogollon ranges, and in extreme southwestern New Mexico near the Arizona and Mexico borders (Ligon, 1961). Ligon indicates a surprising altitudinal range for the species, with the bird occurring at as high as twelve thousand feet in summer and at from five thousand to eight thousand feet during the winter months.

Arizona's population of harlequin quail is found from the Mogollon rim area south to the Mexico border, occurring most commonly in the oak-grassland zone and, to a limited extent, in the pine forests as well (Bishop, 1964). Most of the recent sight records Bishop lists are for Cochise, Santa Cruz, and eastern Pima counties.

The Mexican range of the harlequin quail has been mapped by Leopold (1959), who concluded that it occurs in essentially all the pine-oak upland vegetation from Sonora, Chihuahua, and Coahuila south to near the Isthmus of Tehuantepec in Oaxaca. Binford (1968) reported that in Oaxaca the bird occurs at elevations of from thirty-five hundred to ten thousand feet in air and upland oak scrub vegetation. The southeasternmost locality in the bird's range is La Cieneguilla, Oaxaca. South of the Isthmus in comparable vegetation the ocellated quail occurs in Chiapas. Binford indicated that the northwesternmost locality records for the ocellated quail are near Tapantatepec and north of Santa Effiginia. Thus the two populations are isolated by the tropical lowlands of the Isthmus of Tehuantepec and represent allopatric replacement forms occupying the same habitats and foraging niches. The somewhat intermediate male plumage traits of the Sallé harlequin quail, occurring mostly in Guerrero and Oaxaca, further brings into question the validity of considering the ocellated quail as a distinct species. Thus, it shows the reduction of melanism on the underparts which is so
strongly evident in the ocellated quail, as well as the replacement of white spots on the flanks with brown markings.

In Guatemala the ocellated quail occurs in drier parts of the central highlands, on grassy slopes, in fields, and in open pine woodlands mainly between 5,000 and 10,000 feet (Saunders, Halloway, and Handley, 1950). In Honduras it is found in highland (above 750 meters) pine areas, mainly in open or semiopen situations where there is a heavy undergrowth or long grass (Monroe, 1968). In El Salvador it has been reported at elevations of between 6,400 and 7,000 feet in open pine forests, especially where dense bracken, blueberry vines, and similar undergrowth is well developed (Dickey and van Rossem, 1938). The limit of the species' range is reached in southern Honduras and northern Nicaragua.

**POPULATION DENSITY**

Two estimates of population density were provided by Leopold and McCabe (1957). One was an estimate of twenty-six birds per section (27 acres per bird), based on a count of at least forty-five birds on 1,120 acres made by Wallmo (1951) in Arizona. In northern Chihuahua, Leopold and McCabe estimated that at least twenty-eight to thirty adults per section occurred in fairly well populated range, or 21 to 24 acres per bird. Bishop (1964) reported that one study area in Arizona consisting of about 120,000 square yards (24.8 acres) had five pairs at nesting time, or 5 acres per pair. Another study area of about 33 acres had nine pairs in mid-July, or 3.7 acres per pair. Thus, in favored habitats considerable population densities can occur. Fall population densities were estimated by Bishop in two areas. One area of 130 acres had a minimum of forty-five birds, while another of 160 acres had sixty-two birds; thus fall densities may sometimes reach about three acres per bird. Bishop estimated that over a large area the oak-juniper habitat might have averaged about forty birds per square mile in early December of 1963.

Harlequin quail have been reported on various Mexican breeding bird censuses of the Audubon Society, but on none of these has the population been particularly high. Thus, on both a cactus-acacia grassland and a piñon pine-oak woodland area of Durango, the estimated breeding population was 1 male per thirty acres (Audubon Field Notes, 18:560-561, 1964), while on a pine-oak-mesquite grassland ecotone area of fifteen acres the population was also estimated at 0.5 males (Audubon Field Notes, 11:449-450, 1957). Such low breeding densities probably reflect habitat disturbance, particularly grazing effects.
HABITAT REQUIREMENTS

Leopold and McCabe (1957) concluded that the harlequin quail is an "indicator species" of the pine-oak vegetative zone in Mexico but emphasize that it is neither the pines nor the oaks by themselves that comprise ideal quail habitat. Rather, the understory characteristics represent the critical factor, particularly the presence of bulb-bearing forbs and sedges. These plants can tolerate some periodic burning or limited logging but are severely affected by grazing. Grazing also probably reduces cover for escape and nesting, but the critical factor is the loss of plants upon which the harlequin quail depends for both food and moisture.

Bishop (1964) agreed that the harlequin quail could probably get enough moisture from its succulent foods to survive without other free water and noted that in many areas of southern Arizona such water is lacking except during the summer rainy season. He did, however, observe at least one bird drinking from a puddle after a thundershower, and noted that the possible dependent relationship of reproduction to available water in the free state as well as in succulent foods is still not known.

FOOD AND FORAGING BEHAVIOR

Only a few studies of the foods of the harlequin quail have so far been made. Martin, Zim, and Nelson (1951) noted that in a sample of birds collected primarily in winter from Texas, Arizona, and New Mexico, chufa or nut grass (Cyperus) tubers were most important, followed by oaks (acorns), bulbs of wood sorrel (Oxalis), and brodiaea (Brodiaea) and sunflower (Helianthus) seeds. About 70 percent of the winter food samples were of plant origin, with various insects and other arthropods comprising the animal food.

Leopold and McCabe (1957) provided a complete summary of food items found in harlequin quail, based on their own observations and previous studies. They estimated that about 40 percent of the summer foods eaten were of vegetable origin. Although acorns were listed in seven different studies, the major food item would appear to be bulbs, from various lily species (Echeandia, Brodiaea) and especially from the nut grass Cyperus esculentus. Other succulent foods that are dug up are the bulbs of wood sorrel and the tubers of buttercups (Ranunculus). Seeds of legumes, grasses, piñon pine (Pinus edulis), and forbs are used, as well as the fruits of juniper (Juniperus), ground cherry (Physalis), sumac (Rhus), caltrop (Kallstroemia), and various ericad shrubs (Arbutus, Kalmia). During the summer rainy season a variety of insect life is also taken, especially beetles and the larval stages of moths and butterflies.
A monthly analysis of harlequin quail food consumption in Arizona has been made by Brown (1969a), who noted that, by weight, plant material comprised from 90 to more than 99 percent of the monthly samples, with animal materials being of significance only from June through September, when beetles in particular were consumed. The two primary vegetable food sources were wood sorrel bulbs, which occurred in large amounts from June through January, and nut grass (Cyperus esculentus) bulbs, which were equally important from January through April. In April and May seeds (Paspalum, Lotus) and buds (Gilia) were taken in limited amounts, and during July and August the tubers of morning glories (Ipomoea), seeds of Glactia, and fruits of manzanitas (Arctostaphylos) also appeared in the diet.

A similar seasonal food analysis has been provided by Bishop and Hungerford (1965), based on the study of 221 crop contents. Throughout the year the major foods were acorns, bulbs of wood sorrel, seeds, sedge tubers, and insects. During the winter months of January through March, wood sorrel bulbs were the primary food, with other plant materials such as acorns, seeds, and tubers of secondary importance. In April, May, and June an increasing amount of nut grass or sedge tubers were taken, as well as green acorns, and the importance of wood sorrel began to decline. From July through September insects and green acorns made up the bulk of the foods, with Oxalis and Cyperus of minimal significance. However, from October through December these two food sources, as well as acorns, again became the predominant sources of food intake.

In summary, it would appear that for all except the summer months, the availability of Oxalis and Cyperus underground parts is crucial to the survival of the harlequin quail, with acorns and other seeds or fruits of secondary importance.

The typical foraging behavior of these quail has been described by various writers. Leopold and McCabe (1957) noted that the birds typically dig a hole about two inches long, an inch across, and two or three inches deep, while extracting bulbs. They do not eat the dried hulls, and leave them near these diggings. When eating acorns, the birds also open the hull and remove the meaty center.

Bishop (1964) also noted that when Oxalis bulbs are dug up the birds make cone-shaped holes, with one side of the cone dug away and the bulb hulls left in the hole. When searching for foods nearer the surface the birds made fan-shaped depressions about one-eighth inch deep in duff and litter under bushes and trees, which sometimes covered several square yards in area. He noted that the birds often scratched with one foot and then the other, with frequent pauses to examine the scratched area for foods. Often
the members of a covey fed so closely together that they touched one another, apparently without hostility, with up to eight feeding in a circle only fourteen inches in diameter. He observed that birds apparently fed throughout the day, and only those that were collected after 3:00 P.M. had full crops.

**MOBILITY AND MOVEMENTS**

Nearly all observations of harlequin quail indicate that they are not highly mobile. In spite of their strong legs they do not run when disturbed but rather tend to squat and "freeze." When flushed, they usually fly only fifty to one hundred yards (Leopold, 1959). Bishop (1964) noted that the birds were usually less than twenty feet away when they were flushed and flew no more than one hundred yards, after which they would run rather than fly again. At least on the winter range, coveys apparently return day after day to the same foraging place, and the covey home range may be no more than two hundred yards in radius (Leopold and McCabe, 1957). It is not uncommon to find a covey using the same fifteen yards of a canyon area on consecutive days or at greater intervals (Miller, 1943).

In New Mexico as well as elsewhere a definite altitudinal movement between summer and winter has been noted (Ligon, 1961; Leopold and McCabe, 1957), however, these appear to be relatively short movements, probably not exceeding a few miles. Bishop's (1964) study did not indicate such a seasonal migration; areas which contained birds prior to the nesting season had all supported coveys during the previous hunting season. As the nesting season approached the birds moved decreasing amounts, and he found no evidence that either member of a pair moved more than 150 yards from a nest site. Shortly after hatching the brood range was even less than this; as the chicks grew it gradually increased but even then did not exceed an area of more than 200 yards' radius.

**SOCIAL AND REPRODUCTIVE BEHAVIOR**

While in coveys during the nonbreeding season, the birds form small flocks that probably represent family groups. Leopold and McCabe noted that the average covey size of sixty-two coveys was only 7.6 birds, and rarely have groups of more than 25 ever been reported. These coveys spend the day following a usual activity pattern of morning and evening foraging, with the intervening hours spent resting, dusting, and preening, with some digging for food. During rainy weather they may remain huddled together, and at night they roost on the ground, often facing outward in a semicircle around a rock or a grass clump (Bishop, 1964).
Pairing evidently occurs well before the nesting season actually is underway. Records summarized by Leopold and McCabe (1957), and observations by Bishop (1964), indicate that most pairing in Arizona may occur during March through May, beginning as early as February. In spite of this early pairing, gonadal development does not usually begin until June, with the earliest Arizona records for broods occurring about mid-June, and eggs being found as late as September 20 (Wallmo, 1954). Bishop (1964) concluded that during his study few females began laying before June 28, and most laying probably occurred during July, or about four months after pairing was initiated. It is believed that nesting in this species is adaptively timed so that broods appear soon after the summer rains have provided new green plant growth and an abundance of insects, although the physiological mechanism of such timing is still obscure (Leopold and McCabe, 1957).

Although lone, presumably unpaired, males began to appear as early as mid-May, Bishop did not hear any male calling until mid-June. Most male calling occurred from late July to mid-August, or during the peak period of incubation. Bishop believed that the majority of calling males were mated ones, but Leopold and McCabe said calling during the breeding season is largely and perhaps entirely by lone males. Bishop indicated that he often heard males calling from fifty to one hundred yards away from nest sites, but attraction to nesting sites is typical of unpaired male quail and need not indicate that the calling bird is the mate of the nesting female. A peak of male calling during incubation on the part of unmated males is also characteristic of several of the United States species (see California quail account), and the incidence of male calling is probably correlated with the gonad cycle.

The participation of the male in nest-building, incubation, and nest defense is still slightly uncertain. One study of captive birds indicated that the male may help to construct the nest, which would be in agreement with observations on *Odontophorus*, which also builds a domed nest. Prior to building the nest a scrape is made, which may be one to three inches deep (Bishop, 1964). The cavity may be five or six inches wide and is lined with vegetative material such as grass or oak leaves and often some down (Wallmo, 1954). The sides of the cavity usually consist of grass stems which may appear to be woven together, and which are roofed over the top of the scrape to form a chamber four or five inches high. The side entrance to the nest is often well hidden by a mat of grass stems that hang down over the entrance. Bishop reported that this mat acts like a hinged door, so that it falls back into place whenever the female enters or leaves the nest.

The average clutch size is reported by Leopold and McCabe to be 11.1.
with an observed range of 6 to 14 eggs (Leopold and McCabe, 1957). The egg-laying rate of wild females is as yet unrecorded, but three captive females in the collection of F. S. Strange laid 87 eggs during a sixty-one day period, averaging about three days per egg. During 1967 and 1968, egg laying by his birds consisted of the following monthly totals: 7 in May, 45 in June, 42 in July, 20 in August, and 6 in September.

Bishop never observed males on or very near the nest, but Willard (in Bent, 1932) reported seeing males sitting on eggs in about half of the nests he examined. Males have also been reported sitting close beside incubating hens and without question remain with the female to help guard and rear the young.

The incubation period is probably twenty-five to twenty-six days, which is in general agreement with Odontophorus but longer than the incubation periods of other United States quails (Leopold and McCabe, 1957). Both parents actively participate in brood care; Leopold and McCabe (1957) reported two instances of injury-feigning on the part of the male. The decumbent crest of the male is spread laterally during such disturbances. In eight of ten observed cases, Bishop (1964) noted that pairs with broods under a month old acted in the same fashion, with the female being first to expose herself and attempt to lead intruders away from the brood by feigning a broken wing. If necessary, the male may also appear and behave similarly, after first sending the chicks into hiding by uttering a series of moaning cries. In two instances the male was evidently the first to expose itself and perform distraction displays.

When newly hatched, the birds are fed insects, seeds, and bulbs by the parents, but by the time they are two weeks old they begin to forage for themselves (Bishop, 1964). Probably little brood mixing occurs, since the average reported brood sizes of 6.6 to 8.4 young is not much below the average clutch size (Leopold and McCabe, 1957). However, some broods containing two age-classes have been seen (Wallmo, 1954).

Probably little merging of family units occurs during the fall. Brown (1969b) noted that before the hunting season 70 coveys containing 451 birds occurred on 2.95 square miles, indicating an average covey size of 6.4 birds. These 23.7 coveys per section were thought to be the result of a breeding population of about twenty-four breeding pairs per section. Hunting seasons in Arizona during the years 1965 through 1969 have provided age and sex ratio population data not previously available for the species. Of 4,095 birds shot during these years, 71.5 percent have been young and 56.4 percent have been males (Brown, 1970). This age ratio would represent a juvenile-to-adult ratio of 2.5:1, or more than 5 young raised per adult female on the average, assuming that young birds are not
more vulnerable to shooting than are adults. Comparisons of age ratios based on wing samples with those based on average covey sizes of well-grown broods are in close agreement, suggesting that coveys do consist of family units and probably little differential age vulnerability to shooting exists, judging from data presented by Brown (1969a).

Vocal Signals

The vocalizations of the harlequin quail are neither so loud nor so varied as those of Odontophorus and Dactylortyx, but this is not surprising in view of the relatively more open habitat which the harlequin quail uses and its probable greater reliance on visual signals. Certainly, more plumage dimorphism exists in this species than in any other of the species of the other genera in this subgroup.

Leopold and McCabe described the separation or assembly call of the harlequin quail as a low quavering whistle, with the separate notes slowly descending in pitch. Fuertes (1903) described it as owl-like, and Bishop (1964) reported that it is higher in pitch but lower in volume than the calls associated with the breeding season. The call is uttered by chicks as well as adults of both sexes, although Bishop (1964) indicated that in contrast to Leopold and McCabe he had never heard males produce the call.

Recordings of the separation call made by L. Irby Davis in Jalisco and filed in the Laboratory of Ornithology’s Library of Natural Sounds indicate that this call consists of from six to nine uniformly spaced notes, with each lasting about 0.3 seconds, and the entire series lasting about 2.5 seconds, during which time the fundamental frequency gradually drops from about 4,000 Hz to 3,500 Hz. Eight such call sequences occurred during a 67-second recording period, or about one every 8 seconds.

The second major call is produced by males during the breeding season and is probably an indication of the location of unmated males. Leopold and McCabe (1957) said that it is a high-pitched buzz sound that ascends in pitch rapidly to an inaudible level. In contrast, Bishop described it as a descending whistle combined with a buzzing sound, which can be heard up to 200 yards away under favorable conditions. According to him, a similar call is produced by females, a series of nine high-pitched, low-volume notes of descending pitch, audible up to 150 yards away and resembling the call of the canyon wren (Catherpes mexicanus). Levy, Levy, and Bishop (1966) found that males began to respond to recorded playbacks of this call in June and their period of strongest response was about the beginning of August, or during the period of maximum nesting activity. In contrast to Gambel quail, male harlequin quail would
respond throughout the day to such playbacks. Further, although the
Gambel quail that were attracted were clearly unmated males, these authors
apparently believed that mated male harlequin quail could also be attracted
by such calls.

In addition to these two call-types, a few other vocalizations have been
noted. Conversational or contact notes have been mentioned by a few
workers as occurring when birds were in a covey or foraging, and sometimes
a squealing call is produced when they are flushed (Leopold and McCabe,
1957). Bishop (1964) mentioned that he frequently heard a moaning-crying
sound produced by adults when their young were in danger, and he heard
the same distress call when he picked up crippled or captive birds.

I have had little experience with the harlequin quail and thus cannot
evaluate their vocal similarities to other species. However, while in Chiapas
I inquired of several people as to the calls of the ocellated quail. In the
vicinity of San Cristóbal and southward toward the Guatemala border,
where at least until recently the species was fairly common in pine and pine-
oak forests, the local vernacular name for the bird is colonchango, which
I was told referred to the call of the male. A woman in Comitán who had
frequently kept the species in captivity told me further that the male has
a beautiful whistled song, which sounded to her like pico-de-oro. A man
who had obtained a male as a young bird some six months previously told
me that it had just begun to sing about two weeks previously and had two
different calls. One was the col-on-chang'-o song, which no doubt corres-
ponds to the pico-de-oro vocalization, and the other was a vibrating and
whistled preeet. This latter call is probably equivalent to the buzzing call
of the harlequin quail or perhaps to the separation call. While handling the
bird I was unable to stimulate it to utter any distress calls. Because of its
song, the ocellated quail is far more highly valued as a cage bird in that part
of Chiapas than is the local bobwhite, which is much more readily avail-
able and thus more frequently seen as a cage bird.

EVOLUTIONARY RELATIONSHIPS

Most of the anatomical specializations that are exhibited by the harlequin
quail are related to its digging behavior associated with foraging. Miller
(1943) has mentioned its arched back, strong legs, long claws, and dorsally
narrowed pelvis, which are all associated with the strong leg muscles related
to its digging abilities. The posterior iliac crest of Cyrtonyx is the most
highly developed of the entire group and exceeds that of Dactylortyx
(Holman, 1961). Further, in this species the dorsal surface of the postace-
tabular ilium is narrow anteriorly, and it gradually narrows posteriorly
to form a highly elongated, narrow dorsal roof of the posterior process. *Dactylortyx* and *Rhyynchortyx* are like most other New World quail genera in having a moderately broadened anterior face of the postacetabular ilium that narrows abruptly posteriorly, but in these the posterior process of the ilium forms a moderately long, narrow dorsal roof, rather than a short and broad roof (Holman, 1961). *Odontophorus* is variable with regard to this character, suggesting that an evolutionary trend may be traced from *Odontophorus* through *Dactylortyx* and *Rhyynchortyx* to *Cyrtonyx*. The angle of the ischium relative to the iliac crest is also greater in *Cyrtonyx* than in the other genera (Holman, 1961), which is probably also related to muscular digging adaptations.

From these considerations, as well as distributional patterns, ecological and behavioral considerations, and plumage comparisons, I would judge that *Cyrtonyx* evolved from a *Dactylortyx*- or *Odontophorus*-like ancestral type in a forested or woodland environment and gradually became increasingly efficient at surviving in more xeric habitats than were its ancestors. It is the only species of the *Odontophorus* subgroup that has become fully emancipated from a fairly dense forest habitat and thus has extended its range much farther to the north in arid climates than have any of these.