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TAXONOMY AND BIOGEOGRAPHY OF NEW WORLD QUAIL

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Abstract: New World quail are a distinct genetic lineage within the avian order Galliformes. The most recent taxonomic treatment classifies the group as a separate family, Odontophoridae, within the order. Approximately 31 species and 128-145 subspecies are recognized from North and South America. Considerable geographic variation occurs within some species which leads to ambiguity when describing species limits. A thorough analysis of the Galliformes is needed to clarify the phylogenetic relationships of these quail. It is apparent that geologic or climatic isolating events led to speciation within New World quail. Their current distribution suggests that dispersal followed speciation. Because the genetic variation found in this group may reflect local adaption, the effect of translocation and stocking of pen-reared quail on local population genetic structure must be critically examined.

Key words: biogeography, New World quail, Odontophoridae, taxonomy.

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The New World quail are a diverse and interesting group within the avian order Galliformes. They are distributed from Canada south to South America (Fig. 1; Johnsgard 1988). The more common North American species have received much attention from ecologists because they are important game birds (e.g., Rosene 1969, Johnsgard 1973, Leopold 1977, Scott 1985). Taxonomists also have focused on these quail because they are relatively easy to collect, and probably because of their culinary appeal. That is, early bird collectors and ornithologists often collected quail not only because of their scientific value but also because of their fine taste. These collections provided extensive comparative material for taxonomists working in museums (e.g., see Table 1 for a partial list of galliform taxonomic treatments).

Despite widespread interest in New World quail, the systematics of this group are still in debate (e.g., Mayr and Short 1970, AOU 1983, Sibley and Ahlquist 1990). This dynamic state is due, in part, to recent advances in systematic techniques (e.g., Gutiérrez et al. 1983, Sibley and Ahlquist 1990) as well as to debate over the species concept (Mayr and Short 1970, McKitrick and Zink 1988). Major advances in molecular genetics are providing many new insights into the phylogenetic relationships of quail and other birds (Cooke and Buckley 1987, Hillis and Moritz 1990, Sibley and Ahlquist 1990). I predict additional changes will occur in the taxonomy of New World quail as a result of the application of these new molecular techniques.

In this paper I will discuss the most recent taxonomic and systematic treatments of New World quail (Table 2). Next I will outline some proposed hypotheses about quail biogeography and evolution. Finally, I will discuss the relevance of these systematic and biogeographic studies to North American quail management.

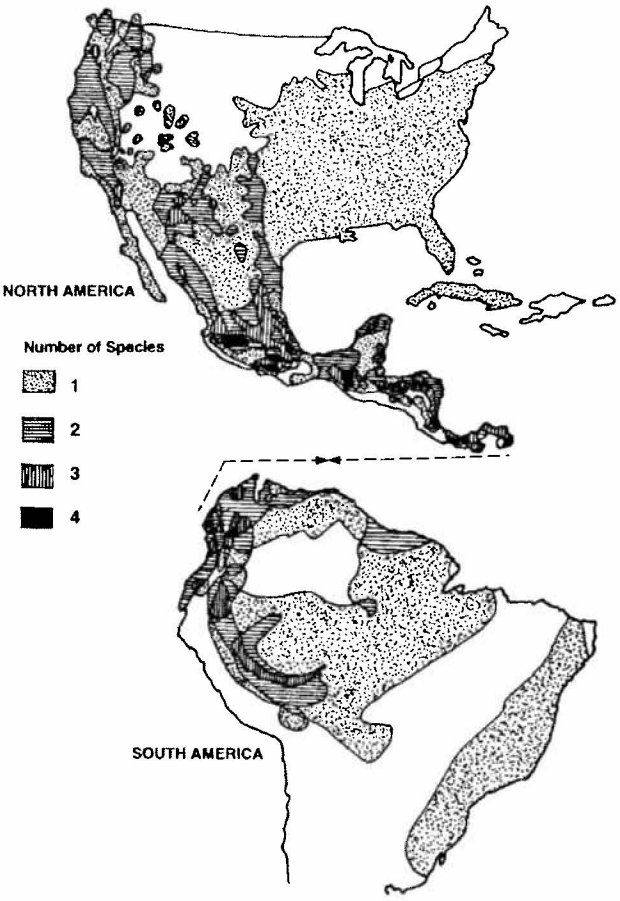

Fig. 1. Distribution and species density of New World quail (after Leopold et al. 1981, Johnsgard 1988).

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to the AOU's committee on nomenclature taxonomic treatment of the odontophorine quail.

TAXONOMY OF NEW WORLD QUAIL

Taxonomy is the study of classifying organisms. Systematics is the study of phylogenetic relationships and evolutionary processes that generate biodiversity. The distinction is important because pure "alpha" level taxonomy may not be sensitive to issues of phylogeny. The most interesting questions in biology are not what an organism's name happens to be, but what are its ecological and evolutionary relationships to other organisms (Brooks and McLennan 1991). Thus most current treatments of taxonomy are really systematic treatments.

Classification of Quail

There have been several taxonomic and systematic treatments of New World quail (Table 1). Until recently most treatments have been based on general morphology (i.e., plumage pattern, color variation, general size) and species integrity (Mayr and Short 1970). Some scientists have based their inferences of relationship on morphology (osteology [Holman 1961]; myology [Hudson et al. 1966]); others have based their inferences on genetic analyses (protein electrophoresis [Gutiérrez et al. 1983]; DNA hybridization [Sibley and Ahlquist 1990]; see also Table 1).

Higher Taxonomic Levels.—All taxonomic treatments of quail place them within the order Galliformes. Sibley and Monroe's (1990) organization (Table 2) is somewhat different than classical approaches because they use a dichotomous classification which requires use of additional taxonomic levels such as "parvorder." This proposed classification is considered to be a working hypothesis by the AOU committee on nomenclature (T. Howell, pers. commun.). Nevertheless, Sibley and Monroe's approach is different from other treatments because they elevate the New World quail to family status (i.e., Odontophoridae). Sibley and Ahlquist (1985, 1990) noted that New World quail were very distinct from other chicken-like birds on the basis of DNA hybridization experiments. The DNA hybridization technique (Sibley and Ahlquist 1990) upon which this classification was based has received widespread criticism among ornithological systematists (e.g., see Lanyon 1992).

Holman (1961) suggested that New World quail should be distinguished as a separate family. He based his suggestion on the significant osteological differentiation exhibited by the New World quail. For example, odontophorine quail are unique among Galliformes by having a serrated mandible. Gutiérrez et al. (1983) also demonstrated that the odontophorine quail were a distinct clade within the Galliformes, but they did not offer a specific recommendation on the family status of the group. Most classification schemes place the New World quail within the subfamily Odontophorinae without substantive comment on the basis for the classification (e.g., Peters 1934, Hudson et al. 1966, AOU 1983), although Delacour (1951) placed them within the subfamily Phasianinae. Despite the large number of studies on species or groups within Galliformes, there is not a comprehensive systematic study of the entire group (see Randi et al. 1991).

Table 1. Major taxonomic treatments of New World quail.

Source	Basis for treatment
Peters (1934)	External morphology
AOU (1957)	External morphology
Holman (1961)	Osteology
Brodkorb (1964)	Fossil record
Hudson et al. (1966)	Myology
Mayr and Short (1970)	External morphology
Sibley and Ahlquist (1972)	Egg white protein electrophoresis
Stock and Bunch (1982)	Cytogenetics
Gutiérrez et al. (1983)	Protein electrophoresis
AOU (1983)	Synopsis of literature
Sibley and Ahlquist (1990)	DNA-DNA hybridization (Sibley and Monroe [1990])

Lower Taxonomic Levels.—Many changes in the taxonomy of species and subspecies of quail have occurred in the past 50 years (Table 2). Initially there was a tendency among taxonomists to describe a newly collected specimen as a new species when it has morphologically differentiated from other specimens. As the biology and distribution of these species became known in greater detail, many of the originally named species were relegated to subspecific status. This process continues today as poorly known species in the Neotropics become known (e.g., *Odontophorus*). There also has been a general trend in ornithology to dissolve monotypic genera. The recent merging of the *Lophortyx* quail (AOU 1957) with *Callipepla* is an example of this trend as it affects American quail.

Table 2. Taxonomies of New World quail.[a]

	Peters (1934)	Howard and Moore (1991)	Sibley and Monroe (1990)
Parvclass	—	—	Galloanserae
Superorder	—	—	Gallomorphae
Order	Galliformes	Galliformes	Galliformes
Parvorder	—	—	Odontophorida
Superfamily	Phasianoidea	—	—
Family	Phasianidae	Phasianidae	Odontophoridae
Subfamily	Odontophorinae	Odontophorinae	—
Genera			
	Dendrortyx (4,8)[b]	*Dendrortyx* (3,8)	*Dendrortyx* (3)
	Oreortyx (1,3)	*Oreortyx* (1,4)	*Oreortyx* (1)
	Callipepla (1,3)	*Callipepla* (1,4)	*Callipepla* (4)
	Lophortyx (3,10)	*Lophortyx* (3,16)	—
	Philortyx (1,1)	*Philortyx* (1,1)	*Philortyx* (1)
	Colinus (4,33)	*Colinus* (3,42)	*Colinus* (3)
	Odontophorus (16,19)	*Odontophorus* (14,20)	*Odontophorus* (15)
	Dactylortyx (1,7)	*Dactylortyx* (1,11)	*Dactylortyx* (1)
	Cyrtonyx (3,6)	*Cyrtonyx* (3,5)	*Cyrtonyx* (2)
	Rhynchortyx (1,4)	*Rhynchortyx* (1,4)	*Rhynchortyx* (1)

[a]These are a few examples of New World quail classifications. An extensive chronology of classifications is presented by Sibley and Ahlquist (1990).

[b](Number of species, number of subspecies); no subspecies given by Sibley and Monroe (1990).

The issue of species and subspecies identity and classification is a focal point of debate in ornithology (Barrowclough 1982, Gill 1982, Johnson 1982, Lanyon 1982, Mayr 1982, Monroe 1982, O'Neil 1982, Parkes 1982, Phillips 1982, Storer 1982, Cracraft 1983, McKitrick and Zink 1988). At issue is the species concept itself. Two systematic constructs, among several, at debate are the biological species concept (Mayr 1969) and the phylogenetic species concept (Cracraft 1983, McKitrick and Zink 1988). In the former the species is recognized on the basis of its genetic isolation from other species. In the latter a species is recognized on the basis of its genetic integrity (McKitrick and Zink 1988) and its evolutionary history. Mayr and Short (1970) attempted to demonstrate that few problems in taxonomy occurred when applying the biological species concept to North American birds. However, because quail readily hybridize both in the wild (Henshaw 1885, Peck 1911, Bailey 1928, Aiken 1930) and in captivity (Johnsgard 1971), Mayr and Short (1970) inferred that American quail were extremely similar and some forms could be conspecific (e.g., *Callipepla californica* and *C. gambelii*) or congeneric (e.g., *Oreortyx pictus* and *C. californica*; Mayr and Short [1970:42]). Although *C. gambelii* x *C. californica* occasionally hybridize there is no widespread introgression. Further, Gutiérrez et al. (1983) demonstrated that *Oreortyx* was distantly related to *Callipepla*. The propensity to hybridize in zones of habitat transitions would not necessarily confuse the taxonomy of the group under the phylogenetic species concept (McKitrick and Zink 1988).

There are currently approximately 128-145 subspecies among the 31 species of extant quail (Johnsgard 1988). In my opinion the validity of many of the subspecies should be questioned. It is clear that some species exhibit a high degree of morphological differentiation (particularly *Colinus*) which facilitates subspecies recognition; but others (e.g., *Callipepla californica*) have many subspecies with relatively little morphological differentiation (Gutiérrez et al. 1983, Zink et al. 1987). Because of these and other problems the trinomial in bird taxonomy has been discussed at length (see Auk 1982:593-615), and proponents of the phylogenetic species concept have suggested abolishing subspecies entirely (Cracraft 1983, Mckitrick and Zink 1988).

Like higher levels of organization in quail taxonomy, much work remains to be done at the lower levels to resolve species limits and subspecies differentiation. In fact, a thorough review of the *original* literature of quail taxonomy would prove fruitful. For example, Browning (1977) noted that subspecific taxonomy of the 2 northern forms of *Oreortyx* has been perpetuated incorrectly over the years. Unfortunately, these errors have not been purged in recent discussions of quail taxonomy (e.g., Johnsgard 1988). The extent to which additional taxonomic and phylogenetic problems exist is unknown.

Genetic Variation in Quail

Genetic variation in and among wild vertebrate populations has been the subject of much research using modern biochemical techniques in the past 15 years (e.g., Nevo 1978, Avise and Aquadro 1982, Smith et al. 1982, Barrowclough et al. 1985, Barrowclough and Johnson 1986) because of its fundamental evolutionary importance (Lewontin 1974). Many techniques are now available that allow not only direct assessment of genic variation but also levels of gene flow and rates of evolution and divergence (Hillis and Moritz 1990). These techniques have allowed systematics and evolutionary biologists to draw inferences about the phylogenetic relationships and biogeography of birds (e.g., Gutiérrez et al. 1983, Zink et al. 1987). Thus far, genetic variation in some odontophorine quail has been assessed using allozyme electrophoresis in only 4 studies (Gutiérrez et al. 1983, Zink et al. 1987, Ellsworth et al. 1988, 1989).

Gutiérrez et al. (1983) observed that Galliformes representing Old World pheasants, Old World quail and partridges, grouse, and New World quail had relatively low levels of genetic variation compared to passerine birds (Barrowclough 1983). However, they were similar to other nonpasserine birds (Barrowclough et al. 1981). Low levels of electrophoretic variation do not imply necessarily a general lack of genetic variation (see Barrowclough and Gutiérrez 1990). In general, nonpasserine birds also may differ in genetic structure from passerine birds because of differences in their demography and life history patterns (see Zink et al. 1987). The odontophorine quail, which included all of the extant species found in the United States, examined by Gutiérrez et al. (1983) had levels of genetic variation similar to other populations of California quail (Zink et al. 1987) and northern bobwhite (*Colinus virginianus*; Ellsworth et al. 1988, 1989).

The studies of Zink et al. (1987) and Ellsworth et al. (1989) are of particular interest because they attempted to partition genetic variation among their study populations. In both studies there was not a strong population structure; however, populations also were not completely panmictic. In Zink et al.'s (1987) study the populations examined occurred over 2,000 km of range, whereas Ellsworth et al. (1989) examined local populations. The failure to detect strong population structure could be related to the technique (i.e., electrophoresis) or the moderate levels of gene flow among populations detected in both studies (see also Zink 1991). Nevertheless, heterogeneity detected among the populations' genetic structures (see also Appendix 2 in Gutiérrez et al. 1983) suggests that this issue should be reassessed using more sensitive genetic techniques (e.g., DNA sequencing).

The large number of subspecies described among the odontophorine quail is a reflection of geographic variation in plumage patterns. Plumage coloration and patterns can be genetically or environmentally controlled (James 1983). In the case of *Colinus virginianus* the degree of plumage variation is great across its geographic range. If the plumage variation in this species is the result of isolation or adaptation to local environments (i.e., it is found in temperate, arid, subtropical, and tropical habitats), genic differentiation is likely to be detected using more sensitive genetic tools.

BIOGEOGRAPHY OF QUAIL

Based on Holman's (1961, 1964) extensive osteological study, the Odontophoridae is a monophyletic group consisting of an *Odontophorus* subgroup (containing *Odontophorus*, *Dactylortyx*, *Cyrtonyx*, and *Rhynchortyx*) and a *Dendrortyx* subgroup (containing *Dendrortyx*, *Philortyx*, *Oreortyx*, *Colinus*, and *Callipepla*). Johnsgard (1988) speculated (but did not test) that the genera *Odontophorus* and *Dendrortyx* represented generalized quail and, thus, most closely approximated the ancestral odontophorine quail. With these generalized quail extant in Central America and with this region having the most taxonomically diverse odontophorine quail fauna (Fig. 1), Johnsgard (1988) suggested that odontophorine quail evolved in Central America.

Gutiérrez et al. (1983) proposed a biogeographic hypothesis for the evolution of the U.S. members of the *Dendrortyx* subgroup of the Odon-

tophoridae using estimates of genetic divergence, inferred from electrophoretic patterns, among *Colinus*, *Oreortyx*, *Callipepla*, and *Cyrtonyx* (which represented the second monophyletic subgroup within the family), calibration of an electrophoretic clock using fossil specimens, and geologic events coincident with divergence times. Under their scenario, *Oreortyx* separated approximately 12.6 million years ago (MYBP), *Colinus* next diverged about 7 MYBP, *Callipepla squamata* separated at approximately 2.8 MYBP, and finally *C. californica* and *C. gambelii* diverged about 190,000 years ago. These divergence times correspond generally with reconstructed geologic and climatic events (Gutiérrez et al. 1983). Hubbard (1973) proposed another vicariant explanation for the evolution of *Callipepla*. He proposed a trichotomous split in which *C. squamata*, *C. douglasii*, and "pre-*C. californica-gambelii*" diverged first in the Illinoian glacial epoch followed by differentiation of *californica* from *gambelii* during the Wisconsinian glacial period. It is possible that climatic influence of Illinoian epoch on vegetation (Axelrod 1979) may have influenced speciation of *C. californica* and *gambelii* but probably not *squamata*. Nevertheless, it is clear that isolation events probably led to the speciation of New World quail. The current distribution (i.e., sympatry) of these species also suggests dispersal subsequent to speciation (Nelson and Platnick 1981). Nevertheless, these are biogeographic hypotheses which cannot be precisely reconciled with paleobotanical and geologic events. In addition, the remaining taxa within the Odontophoridae should be examined to derive approximations of their evolutionary histories and as a test of the above hypothesis (Gutiérrez et al. 1983).

RESEARCH AND MANAGEMENT IMPLICATIONS

Systematic and Taxonomic Investigations

It is evident that thorough analysis of the quail would greatly clarify relationships within Odontophoridae. Genetic assessment techniques now available could be used to clarify not only phylogenetic relationships but also levels of variation within and among species and populations of these fine game birds. A review of the type I envision should include all extant forms of quail in addition to a thorough review of the literature to trace the appropriate nomenclature (sensu Browning 1977). This information could provide the basis for more informed management of these quail as I suggest below.

Release of Pen-reared Birds

The release of pen-reared quail has occurred for many years as a technique to "augment" natural populations or to increase potential quail harvest (Buechner 1950, Sexson and Norman 1972, Leopold 1977, Roseberry et al. 1987). The artificial propagation and release of quail has been controversial for many years because of its effects on wild populations (Landers et al. 1991) and the low survivorship of pen-reared birds.

Although deleterious genetic effects of cultured salmon on native fish stocks is well known in the fisheries literature (e.g., Waples 1991, Hindar et al. 1991), little is known of genetic effects on native populations of releasing large or small numbers of pen-reared quail despite a long history of such introductions. In fact, few studies have been conducted on any aspect of genetic relationships between pen-reared and wild quail (Ellsworth et al. 1988, Wooten 1991).

Leopold (1977:15) argued that natural selection would soon remove maladapted hybrid California quail produced by interbreeding of native and exotic stock from the population, and thus, any deleterious genetic effects would not be felt in a population. Although this may be true of small local introductions, it is unclear if the effect of continuous large-scale introductions in areas of low native quail population density would be equally benign. The experience of our fisheries colleagues should have stimulated our investigation of the genetic effect of introductions on native populations long ago.

I suggested above that the differentiation observed in quail was probably the result of past isolation. This differentiation appears to be greatest in the northern bobwhite. If this divergence during isolation also resulted in local adaptations to environmental conditions, then widespread, intensive releasing of captive or nonnative stock could have potential deleterious genetic effects. Brennan (1991) documented the decline of quail nationally. For example, the northern bobwhite is declining in all areas of its range including those where quail management is a featured land management activity. A comprehensive search for causative factors of this decline must include the effect of genetic mixing of populations. Genetic markers may be identified in wild and introduced birds (Wooten 1991) to trace the introgression of genes into the wild population. Genetic studies should complement

studies of reproductive performance and survival to establish a causal link between changes in demography and changes in genetic structure resulting from introduction of nonnative birds.

Translocating Quail

Brennan (1991) noted the importance of transferring wild-trapped birds as sources of stock for quail populations extirpated by loss of habitat, stochastic demographic events, or severe weather. If suitable habitat returns or remains following 1 of these events, translocation of quail may be a relatively inexpensive technique for reestablishing a population. However, because of the genetic and behavioral differences between pen-reared and wild birds (Roseberry et al. 1987), only wild caught birds should be used in these endeavors. In addition, populations of the same genetic structure from as close as possible to original populations should be the source of the translocations. Widespread genetic screening of populations is possible with relatively little cost if the objective is to document genetic structure of populations within general geographic areas.

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