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Grouse and Quails of North America, by Paul A. Johnsgard

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1 Evolution and Taxonomy

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Part I

Comparative Biology

1

Evolution and Taxonomy

EVOLUTIONARY HISTORY

THE modern array of grouse-, quail-, and partridge-like species occurring in North America is the result of three processes: evolution and speciation within this continent, range expansion or immigration from Central America and Eurasia, and recent introductions by man. The last category accounts for the presence in North America of the chukar and gray partridges, which are both natives of Europe or southern Asia and typical representatives of the quail-like and partridge-like forms that have extensively colonized those land masses. It is still necessary to account for the presence of the nine or so species of grouse-like forms that are native to this continent, as well as the fourteen or fifteen species of New World quails that occur north of the Guatemala-Mexico border. In general, the evidence clearly indicates that the New World quails had their center of evolutionary history and speciation in tropical America, whereas the grouse are a strictly Northern Hemisphere group that perhaps originated in North America but which now occur throughout both this continent and Eurasia and at present represent about an equal number of species in each of the two hemispheres. North America therefore has provided the common ecological conditions to which two distinctly different groups of gallinaceous birds have become independently adapted and have undergone somewhat convergent evolutionary trends.

The evolutionary history of grouse- and quail-like birds on this continent

is a long one, going back to at least Oligocene times, from which an indeterminate quail-like fossil is known, an addition to a unique fossil quail genus *(Nanortyx)* (Tordoff, 1951). Perhaps *Paleophasianus* from the Eocene represents the earliest grouse-like fossil (Holman, 1961), although it is more probably a species of limpkin (Cracraft, 1968). Other known North American fossil species are summarized in table 1. According to Larry

TABLE 1

FOSSIL QUAILS AND GROUSE FROM NORTH AMERICA*

	Quails	*Grouse*
Lower Oligocene	*Nanortyx inexpectatus* Weigel	
Lower Miocene	*Miortyx aldeni* Howard	*Palaealectoris incertus* Wetmore
Middle Miocene	*Cyrtonyx cooki* Wetmore *Miortyx teres* A. H. Miller	*Tympanuchus stirtoni* A. H. Miller
Upper Miocene		*Archaeophasianus roberti* (Stone) *Archaeophasianus mioceanus* (Shufeldt)
Middle Pliocene	*Lophortyx shotwellii* Brodkorb	
Upper Pliocene	*Colinus hibbardi* Wetmore	
Lower Pleistocene		*Tympanuchus lulli* Shufeldt
Middle Pleistocene	*Colinus suilium* Brodkorb	*Palaeotetrix gilli* Shufeldt†
	Neortyx peninsularis Holman	*Dendragapus nanus* (Shufeldt)‡
		Dendragapus lucasi (Shufeldt) *Tympanuchus ceres* (Shufeldt) (also upper Pleistocene)
Total fossil genera	3	3
Total modern genera	3	2
Total fossil species	8	9
Neospecies from archeological sites	6	7

*Based on Holman, 1961, Brodkorb, 1964, and Howard, 1966

†*Dendragapus gilli* according to Jehl, 1969

‡Not separable from *D. lucasi* according to Jehl, 1969

Martin,* the Oligocene and Miocene forms share a number of common characteristics and in general are cracid-like. On this basis it seems a reasonable assumption that both groups may have been derived from cracid-like ancestors during mid-Tertiary times.

The present array of grouse and quail indigenous to America north of Guatemala includes nine species of grouse (ten if *Tympanuchus pallidocinctus* is recognized) and fifteen species of quails (fourteen if *Cyrtonyx ocellatus* is not recognized), as shown in table 2. Evidence that North America may be regarded as the evolutionary center of the grouse includes the fact that it has more total genera and more endemic genera than does Eurasia, although the differences are slight. In contrast, Central and South America exhibit the largest total species number of species as well as the largest number of endemic quail species (nearly all of which are in the large genus *Odontophorus*), whereas North America exhibits the largest number of genera and endemic genera. Since the apparently most primitive genera (*Dendrortyx* and *Odontophorus*) are of Mexican or more southerly distribution, it seems apparent that the center of origin of this group must be regarded as Middle American.

TABLE 2

DISTRIBUTION OF EXTANT SPECIES OF GROUSE AND NEW WORLD QUAILS

	Central and South America	*North America*	*Eurasia*	*Total*
Grouse†				
Total genera	—	5	4	6
Endemic genera	—	2	1	—
Total species	—	9	9	16
Endemic species	—	7	7	—
Quails				
Total genera	6	8	—	9
Endemic genera	1	3	—	—
Total species	20	14	—	30
Endemic species	15	10	—	—

†Based partly on Short, 1967; *T. pallidocinctus* not recognized by him.

It is difficult to determine which of the extant genera of grouse is most like the ancestral grouse types. Short (1967) argues the *Dendragapus* includes the species that possess a greater number of primitive features than do the species of any other extant genus. However, he also mentions two species

* Larry Martin, 1971: personal communication.

of *Bonasa*, two of *Lagopus*, and one of *Tympanuchus* that exhibit presumably ancestral traits, leaving only the genus *Centrocercus* as a relatively specialized genus. I am inclined to regard *Centrocercus* and *Tympanuchus* as the most highly specialized of the extant genera; both of them presumably evolved independently from forest-dwelling forms as arid habitats expanded during the late Tertiary times. I would similarly favor regarding the Holarctic genera *Dendragapus* and *Lagopus* as being nearest the ancestral types in general morphology, with the tundra-dwelling adaptations of *Lagopus* representing a more recent development than the forest-habitat adaptations of *Dendragapus*. The Holarctic genus *Bonasa* and the Old World genus *Tetrao* can then be considered somewhat more specialized offshoots of ancestral *Dendragapus-Lagopus* stock which have remained adapted to temperate forest habitats. These ideas are summarized in figure 1, which provides a suggested evolutionary tree for the extant grouse genera. This diagram seemingly differs considerably from that proposed by Short (1967), but actually represents an only slightly different way of emphasizing what are essentially very similar ideas. Our suggested sequences of genera are identical except for the position of *Centrocercus*, which I believe should be listed adjacent to *Dendragapus* to emphasize better its independent origin from *Tympanuchus*.

Similarly, the extant species and genera of New World quails can be grouped by their relatively primitive or specialized characteristics. There can be little question that the arboreal and long-tailed forms in the genus *Dendrortyx* exhibit a large number of generalized traits, and must therefore be regarded as nearest the hypothesized ancestral quail type. Holman (1961, 1964) reported that this genus exhibits numerous skeletal characteristics suggestive of those found in less advanced gallinaceous families, and, in addition, is the most aberrant extant genus of the group. Second only to *Dendrortyx* in generalized characteristics is the large and similarly forest-adapted but more ground-dwelling genus *Odontophorus*, which shares several primitive traits with *Dendrortyx*. Both genera also exhibit distribution patterns that center in Middle America or northern South America, the presumed area of evolutionary origin of the group.

From this central cluster of forms, it is relatively easy to derive, on zoogeographical, anatomical, and ecological grounds, two independent evolutionary lines in the New World quails. One such line leads in a generally northerly and more xeric-adapted direction, and presumably gave sequential rise to *Philortyx*, *Oreortyx*, *Callipepla*, and *Colinus* (which also moved south), as suggested in the accompanying evolutionary tree (fig. 1). The genus *Philortyx* is clearly transitional in its morphology and other characteristics between the suggested ancestral quail and these specialized

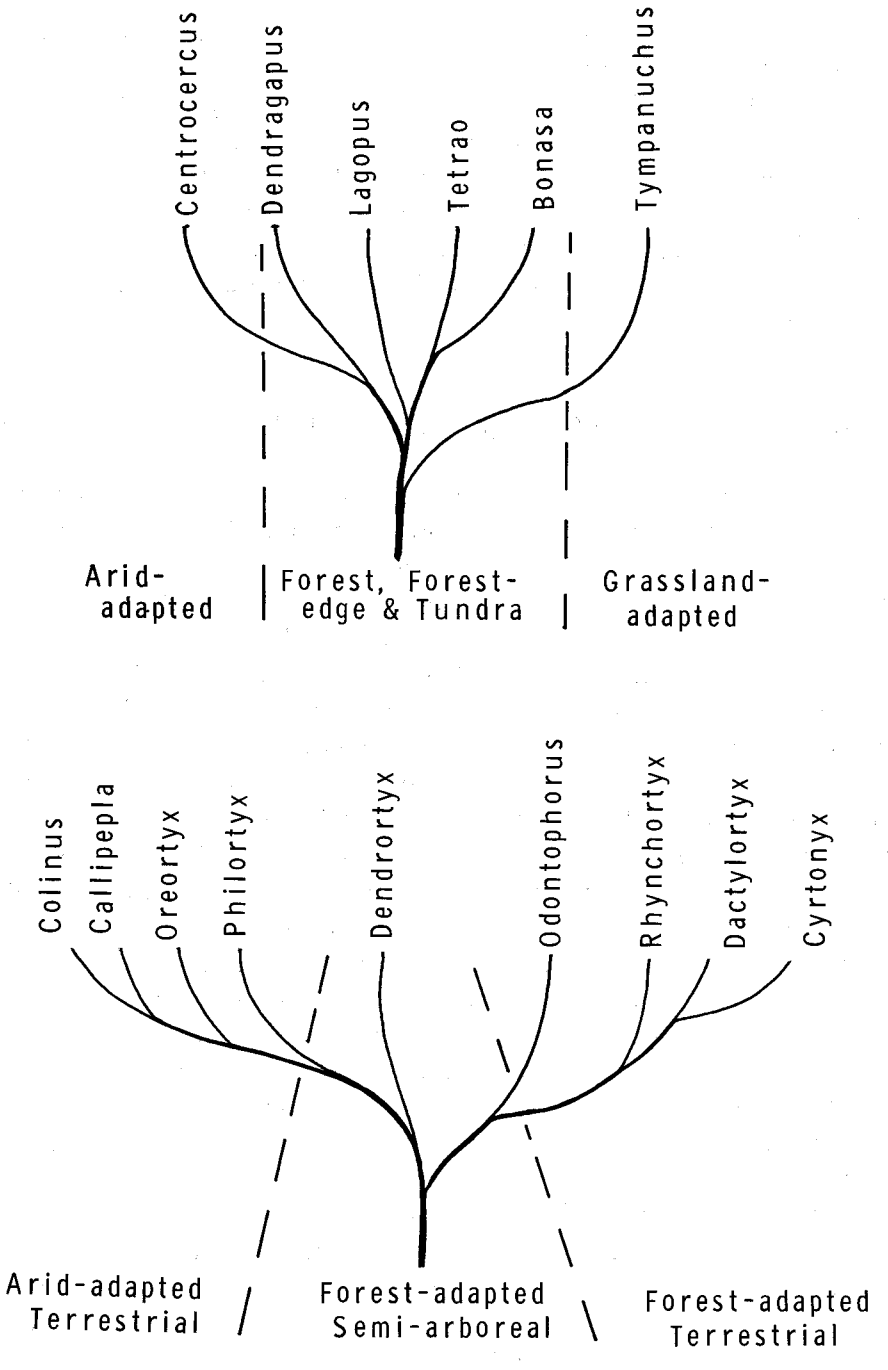

FIGURE 1. Evolutionary tree of extant genera of grouse (above) and quails (below).

and crested types, which are mostly seed-eating forms associated with open and often arid habitats.

From the *Odontophorus* nucleus, it is likewise fairly easy to derive the remaining three genera, *Dactylortyx*, *Cyrtonyx*, and *Rhynchortyx*. These are mostly Middle American forest dwellers that are in two cases relatively more specialized for digging for bulbs, rootlets, and tubers than for seed-eating. The long-legged and weak-toed *Rhynchortyx* differs in this regard, but nonetheless exhibits distinct skeletal similarities to *Cyrtonyx* and *Dactylortyx* (Holman, 1961).

GENERAL TAXONOMIC SEQUENCE AND HIGHER CATEGORIES

Until fairly recently, the traditional American treatment of the grouse has been to designate them as a distinct family, Tetraonidae, although the 1886 *A.O.U. Check-list* also included the New World quails in this family. Familial recognition of both the Tetraonidae and the Odontophoridae occurred with the third edition of the *A.O.U. Check-list* in 1910 and in the case of the grouse has persisted ever since. Other major authorities who have given a corresponding ranking to the grouse include Peters (1934), Ridgway and Friedmann (1946), Wetmore (1960), and Hudson et al. (1966). But recently a number of other writers have urged a reclassification of the group as a subfamily (Tetraoninae) of the Phasianidae. Some of the authors who have supported this view include Delacour (1951), Mayr and Amadon (1951), Sibley (1960), Brodkorb (1964), Holman (1964), Streseman (1966), Short (1967), and others. Hudson et al. (1966) admit that their basis for retaining familial status for the grouse is rather weak; it apparently stems in part from the fact that the grouse genera they studied were obviously much more closely related to one another than they were to any other genera. This would not seem to be sufficiently strong reason to maintain the family, in my view, nor would the obviously adaptive feathered condition of the tarsus and nostrils and the pectinate toes seem to justify such separation.

The level of separation of the New World quails is somewhat more difficult because of problems of separating real phyletic affinities from convergent similarities between this group and the Old World partridges and quails. Apart from occasional familial separation (Odontophoridae), as used for example in the 1910 edition of the *A.O.U. Check-list*, the group has generally been included in a subfamily of the Phasianidae. This was the procedure followed by Peters (1934), Ridgway and Friedmann (1946), Mayr and Amadon (1951), Sibley (1960), Brodkorb (1964), Holman (1964,

but not 1961), Hudson, Lanzillotti, and Edward (1959), Hudson et al. (1966), Short (1967), and others. In these cases the Old World quails either were regarded as a separate subfamily, Perdicinae (Ridgway and Friedmann, 1946), or were more commonly included in the large subfamily Phasianinae (e.g., Peters, 1934; Sibley, 1960; Holman, 1964; Brodkorb, 1964; Short, 1967). A tribal (Odontophorini) recognition of the New World quails within the subfamily Phasianinae was advocated by Delacour (1961), while Streseman (1966) suggested closer affinities with the Old World quails by listing the New World species as a tribe of the subfamily Perdicinae. This question of relative closeness of relationship to the Old World quails and partridges seems to be the most important criterion in deciding whether the New World quails should be given subfamilial rank or simply listed as a tribe of the Phasianinae. On the basis of chromosomal studies, Jensen (1967) concluded that the New World quails are probably not as closely related to *Coturnix* and Old World partridges as they are to *Phasianus*. Hudson, Lanzillotti, and Edward (1959) and Hudson et al. (1966) reported a considerable number of similarities between New World quails and various Old World forms, particularly *Alectoris*, and seemed uncertain whether subfamilial separation was warranted. Arnheim and Wilson (1967) provide biochemical data suggesting close relationships between representatives of the New World quails and the Old World partridges and quails. Holman's (1961, 1964) evidence on skeletal anatomy, including some fourteen criteria, provides the strongest support for maintaining subfamilial separation and is the primary basis for the classification followed here. It would also seem desirable to distinguish taxonomically the true pheasants and their relatives (as recognized by Delacour, 1951) from the remaining Old World quails, partridges, and francolins, which may perhaps be best achieved by tribal separation, although several genera (*Ptilopachus*, *Ophrysia*, *Galloperdix*, and *Bambusicola*) provide intermediate characteristics.

Finally, it has been urged by several recent writers (e.g., Sibley, 1960; Brodkorb, 1964; Hudson et al., 1966; Streseman, 1966; and Short, 1967) that the turkeys and guinea fowl should probably be given no more than subfamilial recognition, but that the hoatzin (*Opisthocomus*) only very doubtfully belongs in the order Galliformes (Hudson et al., 1966). The summary of galliform classification shown in table 3 takes these recommendations into account.

GENERIC AND SPECIES LIMITS

As with many groups of birds that have been subjected to sexual selection and selection for reproductive isolation in a polygamous or promiscuous

TABLE 3

Summary of Suggested Galliformes Classification

ORDER GALLIFORMES

- Superfamily Cracoidea
  - Family Megapodidae—megapodes or mound builders (10 spp.)
  - Family Cracidae—chachalacas, guans, and curassows (38 spp.)
- Superfamily Phasanoidea
  - Family Phasianidae—pheasant-like birds (199 spp.)
    - Subfamily Meleagridinae—turkeys (2 spp.)
    - Subfamily Tetraoninae—grouse and ptarmigans (16 spp.)
    - Subfamily Odontophorinae—New World quails (30 spp.)
    - Subfamily Phasianinae—Old World pheasants (144 spp.)
      - Tribe Perdicini—Old World partridges, francolins, and quails (95 spp.)
      - Tribe Phasianini—pheasants, peafowl and jungle fowl (49 spp.)
    - Subfamily Numidinae—guinea fowl (7 spp.)

mating system (Sibley, 1957), the classification of the grouse has been confused by a plethora of generic names having little if any phylogenetic significance. Fortunately, Short (1967) has reviewed this situation from the viewpoint of both Eurasian and North American forms and has effectively stated the case in favor of elimination of several unnecessary generic names. Among the North American forms, these include the genera *Canachites (=Dendragapus)* and *Pedioecetes (=Tympanuchus)*. At the species level, the American Ornithologists Union (1957) has already seen fit to merge *Dendragapus franklinii* with *D. canadensis*, and *D. fuliginosus* with *D. obscurus*, as essentially allopatric populations that are best regarded as subspecies.

The only remaining question relative to the grouse is that posed by the "lesser" form of prairie chicken, *Tympanuchus pallidocinctus*, which is still recognized as specifically distinct by the *A.O.U. Check-list*. Short (1967) summarized the evidence favoring the view that this population should likewise be regarded as only racially distinct from *T. cupido* and questioned the evidence presented by Jones (1964a) supporting species separation. More recently, Sharpe (1968) has also contributed his views, which in general are in agreement with those of Jones. The question is one that is impossible to provide with a clear-cut answer, and the conclusion one reaches reflects in large measure one's personal philosophy about the primary function of the species category. No additional evidence on the

question has been gathered in this study, but *T. pallidocinctus* will not be given the space or attention that has been accorded the better-defined species.

Among the quails, problems of generic recognition are limited to relatively few instances. Most authorities (Peters, 1934; Ridgway and Friedmann, 1946; *A.O.U. Check-list,* 1957) recognize the genus *Lophortyx* as distinct from *Callipepla.* An adequate anatomical separation of these two genera has yet to be made, and the biological and anatomical validity of distinguishing them has been recently questioned by Sibley (1960), Holman (1961), Phillips, Marshall, and Monson (1964), Hudson et al. (1966), and others. Delacour (1961, 1962) synonymized both these two genera and *Oreortyx* and *Philortyx* as well but failed to provide adequate reasons for this procedure. I have suggested (1970), as has Holman (1961), that *Colinus* is clearly so closely related to the *Callipepla-Lophortyx* complex that it too is a highly questionable genus. Yet, since such lumping of *Colinus* with these other forms would tend to obscure the close relationships of the three bobwhite species with one another, I have refrained from doing so in this book. It is of some interest that the crested forms of bobwhite were once generically distinguished *("Eupsychortyx")* from the noncrested ones *(Colinus)* in a manner analogous to the separation of *Callipepla* from *Lophortyx* largely on the basis of crest condition.

At the species level, the primary problem concerns the possible justification for recognizing *Cyrtonyx ocellatus* as distinct from *C. montezumae.* This case, like that of the lesser prairie chicken, involves an allopatric population which is clearly a result of fairly recent separation. The biology of *ocellatus* is as yet unstudied, but until it can be proved to the contrary, it would seem most probable that the form should be regarded as a highly distinctive race of *montezumae.* In deference to tradition, however, it is listed separately in this book, although no individual account of its biology will be included.

Similarly, Mayr and Short (1970) have suggested that the Yucatán population of bobwhites *(Colinus nigrogularis)* is probably conspecific with *C. virginianus.* The question is complicated by the presence of a series of highly variable populations of *Colinus* extending from Guatemala all the way to northern Brazil. These have usually been regarded as consisting of two species *(C. cristatus* and *C. leucopogon),* although as many as three species were recognized by Todd (1920). Monroe (1968) has argued for the lumping of these population groups into the single species *C. cristatus,* which thus exhibits as much plasticity in plumage variation in Middle and South America as does *C. virginianus* in Mexico and the United States. I am at present uncertain whether *nigrogularis* is phylogenetically closer

to the *cristatus* group or to *virginianus*, and Holman (1961) reported that in its skeletal anatomy *nigrogularis* exhibits a generally intermediate condition (resembling *virginianus* in four of twelve characters, *leucopogon* in two characters, and being unique in six characters). Cink (1971) reported stronger vocal similarities between *nigrogularis* and *virginianus* than between *nigrogularis* and *cristatus*. A possible extreme solution would be to consider the entire complex of allopatric populations as a single species, but such a position cannot be justified on the basis of current knowledge, and representatives of the extreme types *(virginianus* and *cristatus)* are known to differ considerably in downy plumage, egg coloration, and nearly all vocalizations other than the male *"bob-white"* notes.

On the basis of these considerations, a list of the species included in this book is shown in table 4. Rather than being listed in taxonomic sequence, they have been organized according to zoogeography and the major plant community types with which they are most closely associated. A detailed identification of habitat preferences and range of ecological distributions is not possible in such a tabular comparison, but the individual species accounts in the second section of this book will provide a more accurate analysis of habitat characteristics of each species. What is of interest here is the large number of tropical and arid-temperate community types that have been colonized by the New World quails, and the corresponding habitat segregation in arctic and temperate community types of the North American grouse. Only in the case of the greater prairie chicken and the bobwhite is any ecological overlap indicated in the table, and certainly these two species also exhibit marked niche differences. The general geographic distribution of these vegetational communities is illustrated in figure 2, which has been derived from various sources. With a few exceptions, this map illustrates the distribution of potential climax vegetational types rather than successional or disturbance conditions.

An abbreviated systematic synopsis of the species included in this book follows, with subspecies excluded since they are listed under the individual species accounts:

Family Phasianidae: pheasant-like birds
  Subfamily Tetraoninae: grouse and ptarmigans
    Genus *Dendragapus* Elliot 1864
      (Subgenus *Dendragapus*)
        1. *D. obscurus* (Say) 1823: blue grouse
      (Subgenus *Canachites* Stejneger 1885)
        2. *D. canadensis* (Linnaeus) 1758: spruce grouse
    Genus *Centrocercus* Swainson 1831
        1. *C. urophasianus* (Bonaparte) 1828: sage grouse

Genus *Lagopus* Brisson 1760

1. *L. lagopus* (Linnaeus) 1758: willow ptarmigan
2. *L. mutus* (Montin) 1776: rock ptarmigan
3. *L. leucurus* (Richardson) 1831: white-tailed ptarmigan

Genus *Bonasa* Stephens 1819

1. *B. umbellus* (Linnaeus) 1776: ruffed grouse

Genus *Tympanuchus* Gloger 1842

1. *T. cupido* (Linnaeus) 1758: pinnated grouse
2. *T. phasianellus* (Linnaeus) 1758: sharp-tailed grouse

Subfamily Odontophorinae

Genus *Dendrortyx* Gould 1844

1. *D. macroura* (Jardine & Selby) 1828: long-tailed tree quail
2. *D. barbatus* Gould 1844: bearded tree quail
3. *D. leucophrys* Gould 1844: buffy-crowned tree quail

Genus *Philortyx* Gould 1844

1. *P. fasciatus* (Gould) 1844: barred quail

Genus *Oreortyx* Baird 1858

1. *O. pictus* (Douglas) 1829: mountain quail

Genus *Callipepla* Wagler 1832

(Subgenus *Callipepla*)

1. *C. squamata* (Vigors) 1830: scaled quail

(Subgenus *Lophortyx* Bonaparte 1838)

2. *C. douglasii* (Vigors) 1829: elegant quail
3. *C. gambelii* (Gambel) 1843: Gambel quail
4. *C. californica* (Shaw) 1789: California quail

Genus *Colinus* Goldfuss 1820

1. *C. virginianus* (Linnaeus) 1758: bobwhite
2. *C. nigrogularis* (Gould) 1843: black-throated bobwhite

Genus *Odontophorus* Vieillot 1816

1. *O. guttatus* (Gould) 1838: spotted wood quail

Genus *Dactylortyx* Ogilvie-Grant 1893

1. *D. thoracicus* (Gambel) 1848: singing quail

Genus *Cyrtonyx* Gould 1844

1. *C. montezumae* (Vigors) 1830: harlequin quail
2. *C. ocellatus* (Gould) 1836: ocellated quail

Subfamily Phasianinae: Old World pheasants, partridges, francolins, and quails

Tribe Perdicini: Old World partridges, francolins, and quails

Genus *Perdix* Brisson 1760

1. *P. perdix* (Linnaeus) 1758: gray partridge

Genus *Alectoris* Kaup 1829

1. *A. chukar* (Gray) 1830: chukar partridge

TABLE 4

Ecological Distribution of North American Grouse and Quails

Vegetation or region	*Representative quail*	*Representative grouse*
Tundra		
Alpine		White-tailed ptarmigan
High arctic		Rock ptarmigan
Low arctic		Willow ptarmigan
Coniferous forest		
Western montane		Blue grouse
Northern boreal		Spruce grouse
Hardwood; hardwood-coniferous		
Northern deciduous		Ruffed grouse
Evergreen chaparral	Mountain quail	
Grassland; grassland-forest		
Shortgrass; Brushland		Sharp-tailed grouse
Tallgrass-forest ecotone	Bobwhite	Greater prairie chicken
California grassland	California quail	
Shortgrass-desert ecotone		Lesser prairie chicken
Desert scrub		
Sage; sage grassland		Sage grouse
Sonoran scrub desert	Gambel quail	
Chihuahuan scrub desert	Scaled quail	
Tropical deciduous forest		
Northern Mexico	Elegant quail	
Central Mexico	Barred quail	
Yucatan Peninsula	Black-throated bobwhite	
Pine-oak forest		
Northern Mexico	Harlequin quail	
Southern Mexico	Ocellated quail	
Tropical evergreen forest	Singing quail	
Lowland rain forest	Spotted wood quail	
Cloud forest		
Western Mexico	Long-tailed tree quail	
Eastern Mexico	Bearded tree quail	
Southern Mexico	Buffy-crowned tree quail	

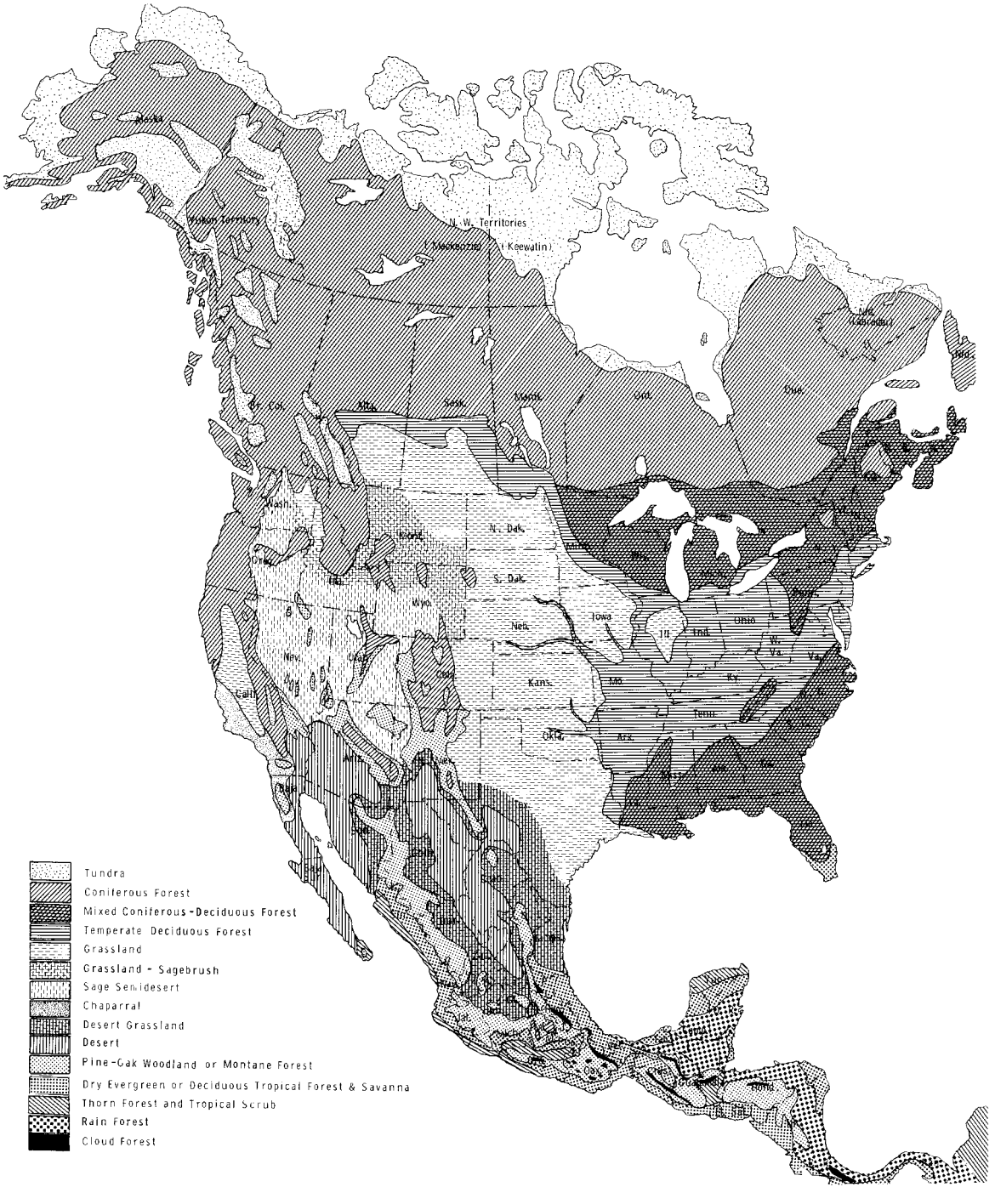

FIGURE 2. Distribution of major natural vegetation communities in North America.