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GEOGRAPHIC ORIENTATION OF AMERICAN TETRAONIDAE

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Abstract: Differentiation of both species and genera within the grouse family (Tetraonidae) has been pronounced in North America. Each of its species has become adapted to specific types of habitat. These vary greatly, from arctic tundra to northern desert scrub and humid forest of both deciduous and coniferous types. All the species are racially variable in some degree, from the sage grouse (*Centrocercus urophasianus*), with 2 races, to the ruffed grouse (*Bonasa umbellus*), with 13. The races tend to be correlated with the ecological climax area in which they live. There are a few cases in which this correlation is not obvious and racial variation seems to be entirely the result of geographical isolation. The present status of grouse depends chiefly on the extent to which modification of required habitat has taken place; the greatest changes have occurred in the grasslands and the least in the arctic–alpine areas.

American grouse occupy a wide range of habitats, mostly of a subclimax or successional stage type, in the arctic and temperate portions of the continent north of Mexico, from the rocky barrens of the Far North and high mountaintops of the West to the prairies of the Gulf Coast. These occupied habitats are representative of most of the major ecological areas of different climax types found within this great expanse of country, although major gaps occur in the evergreen and tropical types of the Southeast, and the southern desert scrub, chaparral, and woodland types of the Southwest (Fig. 1). In this extensive and ecologically varied area, grouse have differentiated into nine species, all but two of which are confined to North America.

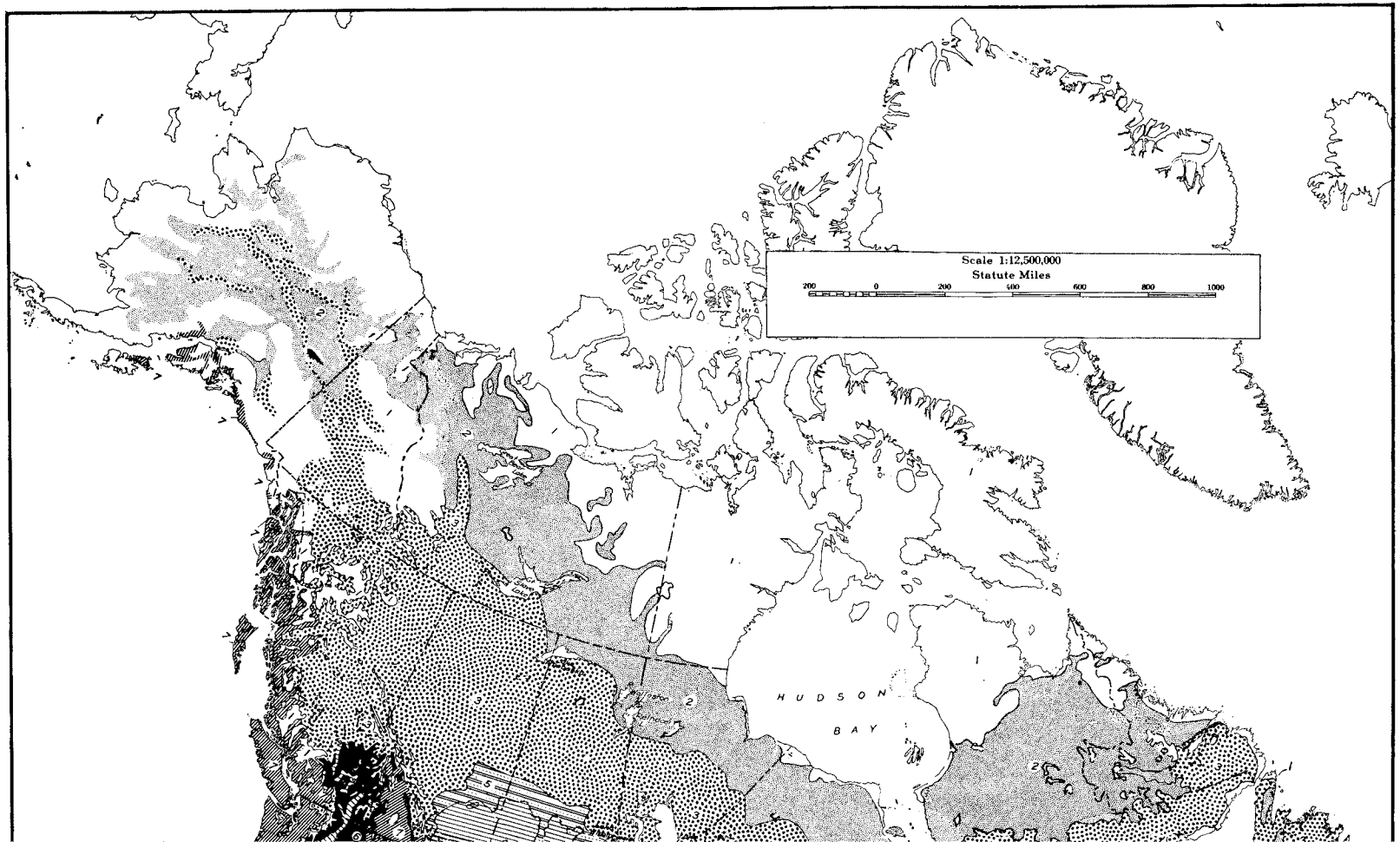
According to the classification of Peters (1934:24–42), which differs from the present arrangement only in recognizing two species of *Canachites* instead of one, there are nine species in seven genera of grouse confined to North America, as compared with eight species in five genera confined to the rest of the world excluding North America. Only two species, the willow and rock ptarmigans (*Lagopus lagopus* and *L. mutus*), are present in both the New and Old Worlds. Thus it would appear that evolution within this family of birds has been very active in the relatively limited geographical area of North America.

Each species of grouse appears to have become adapted to a particular life form of vegetation. There is some overlap, but, by and large, each North American species has its own individual preference for a specific type of habitat. In some places, the preferred forms of vegetation are climax types for the regions where they occur; in other places, they are stages in succession to the climax types. However, even though the species as a whole may occupy habitats of equivalent life form (deciduous, coniferous, etc.) throughout its

GEOGRAPHIC ORIENTATION

Greater prairie chickens, photo by Wilmer D. Zehr, Illinois Natural History Survey, Urbana.

LIFE AREAS OF NORTH AMERICA



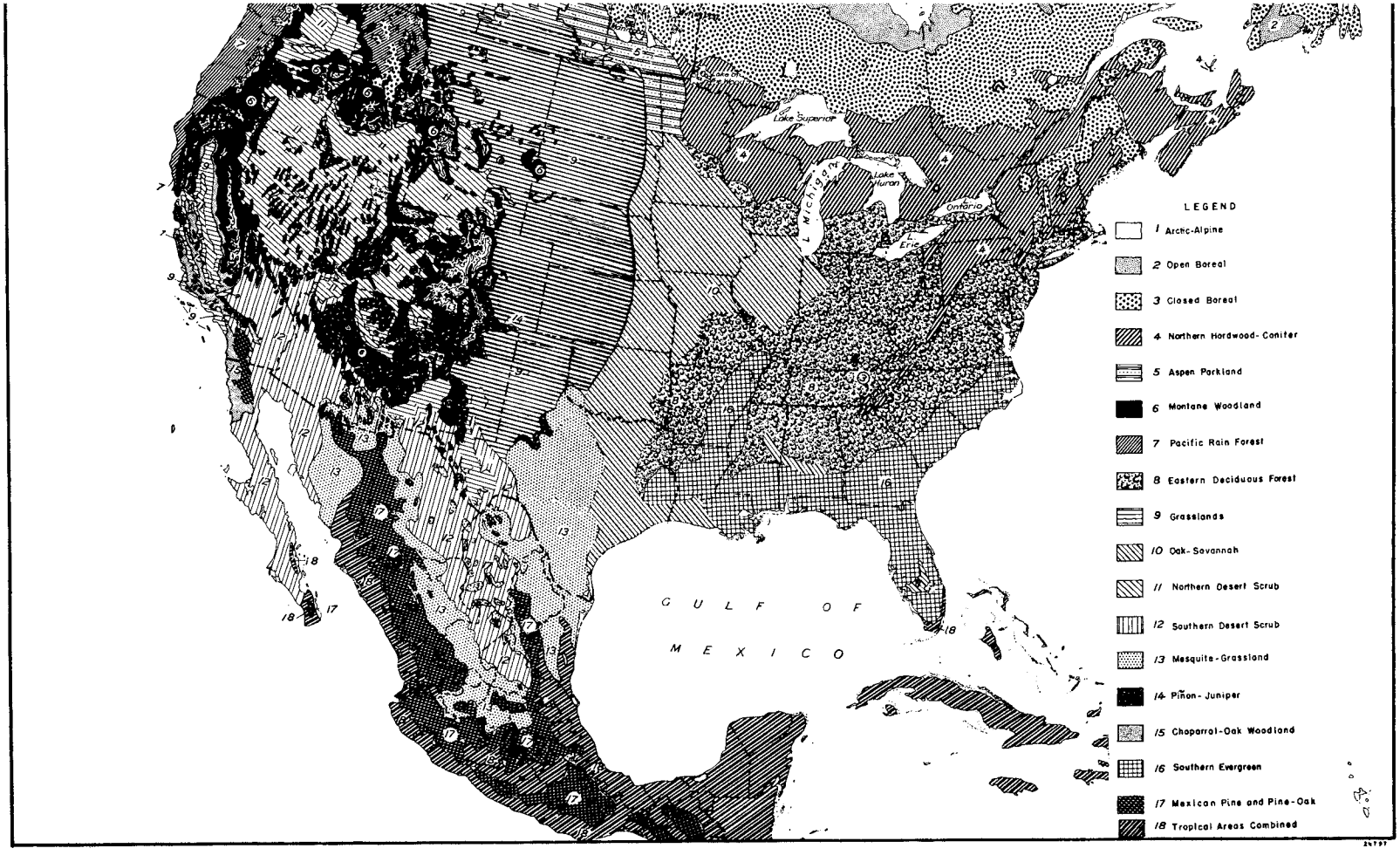


Fig. 1. Life areas of North America.

entire geographical range, if two or more climax areas are included within this range, subspecific variation usually occurs, and this tends to be correlated with progressive changes from one climax to another. In a few species, part of the subspecific variation which occurs has no apparent ecological correlation and presumably is chiefly the result of random variation maintained by geographical separation of populations, which prevents the interchange of genetic characteristics. On the other hand, some of the seeming lack of correlation between morphological variation and ecological distribution is probably due to the incompleteness of our knowledge.

Comparison of maps showing the distribution of the various species and their races (Figs. 2–14) with the map of major life areas based on ecological climax types (Fig. 1) will show which species and subspecies occupy each climax area. The map in Fig. 1 is based on personal observations by the author and many other sources of information, particularly the works of Braun (1950), the Forestry Branch of Canada (1956), Hare (1959), Kendeigh (1954), Leopold (1950), Pitelka (1941), Shantz and Zon (1924), Sigafoos (1954), and Taylor and Little (1950). The concept on which this map is based is essentially that of the biome (Pitelka 1941:115–116) and the biociation (Kendeigh 1954: 166). The application of this concept to the distribution of grouse species has been pointed out previously by Pitelka (1941: 119–124). Although not previously published, this original map is used here in preference to already published versions because it is more up to date with respect to the distribution of climax types, particularly in Canada and Alaska. The names used for the different Life Areas are self-explanatory.

DISTRIBUTION OF SPECIES

The grouse-distribution maps are based chiefly on my personal investigations (Aldrich and Duvall 1955:4–14). Information on distribution of willow and rock ptarmigans, two species which were not covered in the earlier publication, was obtained from various sources in the literature, particularly the American Ornithologists' Union (1957:131–135), Gabrielson and Lincoln (1959:298–310), Peters (1934: 30–35), Ridgway and Friedmann (1946: 97–129), Salomonsen (1950:159–182), and Snyder (1957:112–123). Current information on the distribution of the white-tailed ptarmigan (*L. leucurus*) in Montana was supplied by Thomas S. Choate (Personal communication). All maps in this paper were drawn by Mary W. Mann of the Bureau of Sport Fisheries and Wildlife.

The blue grouse (*Dendragapus obscurus*) is most often found, during the breeding season, in the fairly open coniferous forests of the western mountains and Pacific coastal region (Fig. 2), where it occupies coniferous forest edges and aspen groves, favoring second growth after fires and lumbering (Hamerstrom and Hamerstrom 1961:285), from Yukon Territory south to southern California and New Mexico. It winters in the denser coniferous forest at higher altitudes. There is a general tendency for the considerable subspecific variation to coincide with the climax forest type which characterizes the area where the birds occur, from moist Pacific coastal rain forest to dry Great Basin and southern Rocky Mountain forest types. However, this relationship is obscure over much of the areas occupied, and isolation through separation of montane habitats seems to be an important factor, particularly in the southern part of the range. The distribution of the blue grouse is not known to have changed materially in historic times.

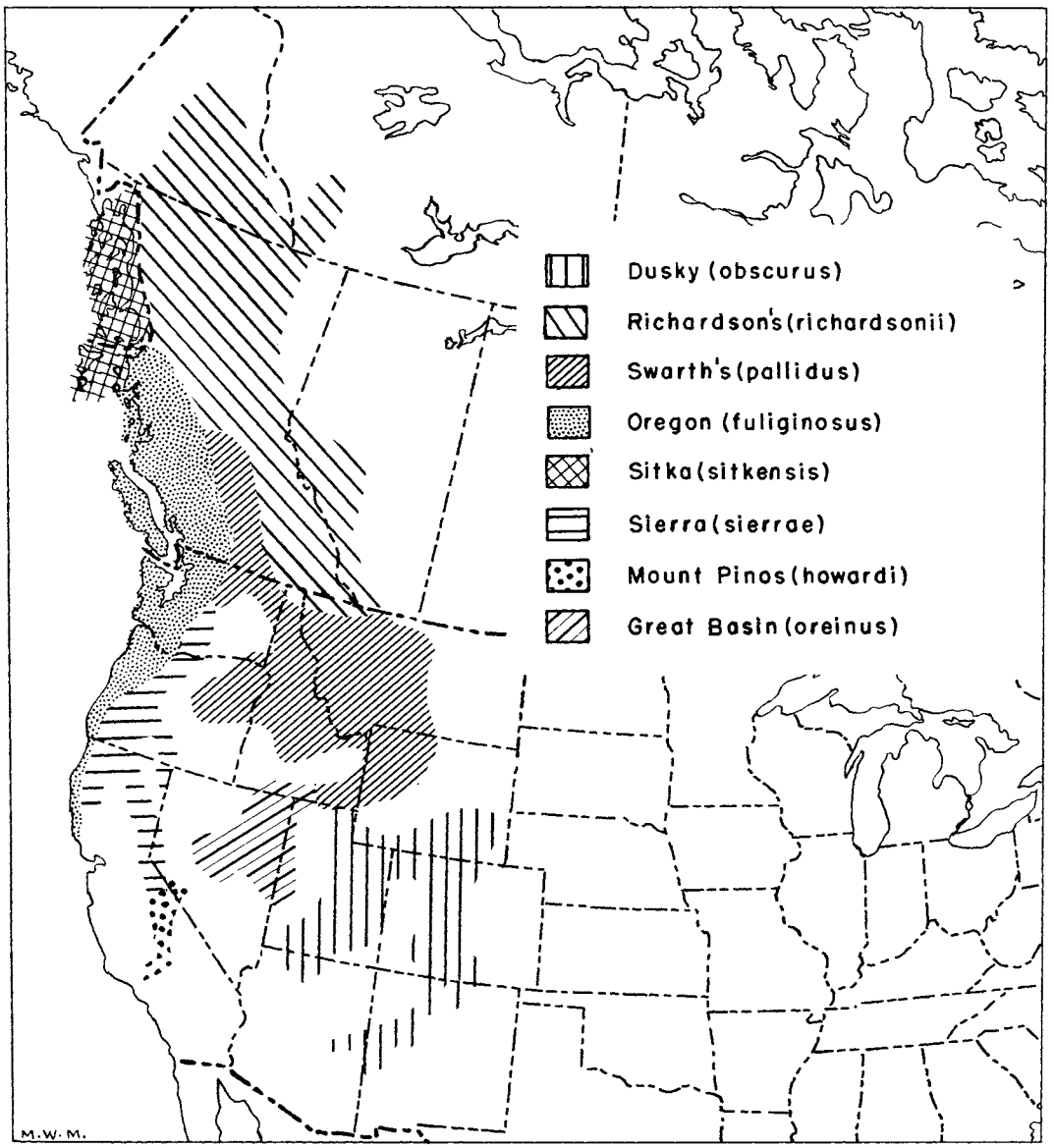


Fig. 2. Blue grouse (*Dendragapus obscurus*), original distribution of subspecies.

The spruce grouse (*Canachites canadensis*) is preeminently a species of the transcontinental boreal forest, including both open and closed boreal areas from Labrador to Alaska (Fig. 3). It extends also into the subalpine equivalent in the Cascades and northern Rocky Mountains. There it is represented by the distinct but intergrading subspecies, Franklin's spruce grouse (*C. c. franklinii*), formerly thought to be a distinct species. Although remarkably uniform racially in the two transcon-

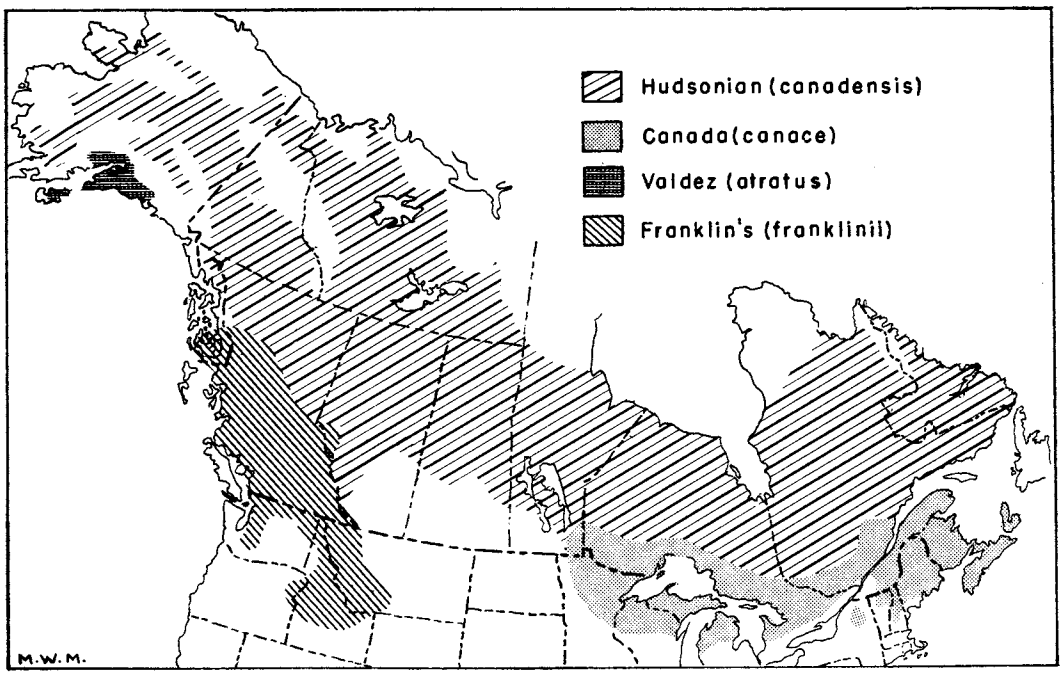


Fig. 3. Spruce grouse (*Canachites canadensis*), original distribution of subspecies.

tinental boreal forest belts occupied by the Hudsonian spruce grouse (*C. c. canadensis*), where this species ranges into the distinctly different northern hardwood–conifer and Pacific rain forest life areas in the Great Lakes–St. Lawrence basin and southern coast of Alaska, respectively, distinct subspecies occur. Throughout its range, the spruce grouse is partial to the heavy, mature coniferous forests of jack pine and spruce–fir, particularly where interspersed with openings caused by burns or bogs. Compared with the ruffed grouse, the spruce grouse varies little geographically, presumably because of the relative uniformity and continuity of its northern coniferous forest habitats. Although spruce grouse have receded northward to some extent with the elimination of their boreal forest habitat, particularly along the southeastern portion of their range, they still occur, at least sporadically, over most of the area they were formerly known to occupy.

The ruffed grouse is one of the most wide-ranging and most racially variable of all American Tetraonidae. Generally found in deciduous habitats, particularly of second-growth types, the ruffed grouse occupies a relatively large number of life areas with which its racial variation seems to be rather well correlated (Fig. 4). For example, the St. Lawrence ruffed grouse (*Bonasa umbellus togata*) lives chiefly in the northern hardwood–conifer area, the eastern ruffed grouse (*B. u. umbellus*) and the Appalachian ruffed grouse (*B. u. monticola*) in the eastern deciduous forest area, the midwestern ruffed grouse (*B. u. mediana*) in the oak–savannah woodlands, the gray ruffed grouse (*B. u. umbelloides*) in the closed boreal area, the Yukon ruffed grouse (*B. u. yukonensis*) in the open boreal area, the hoary ruffed grouse (*B. u. incana*) in the drier montane wood-

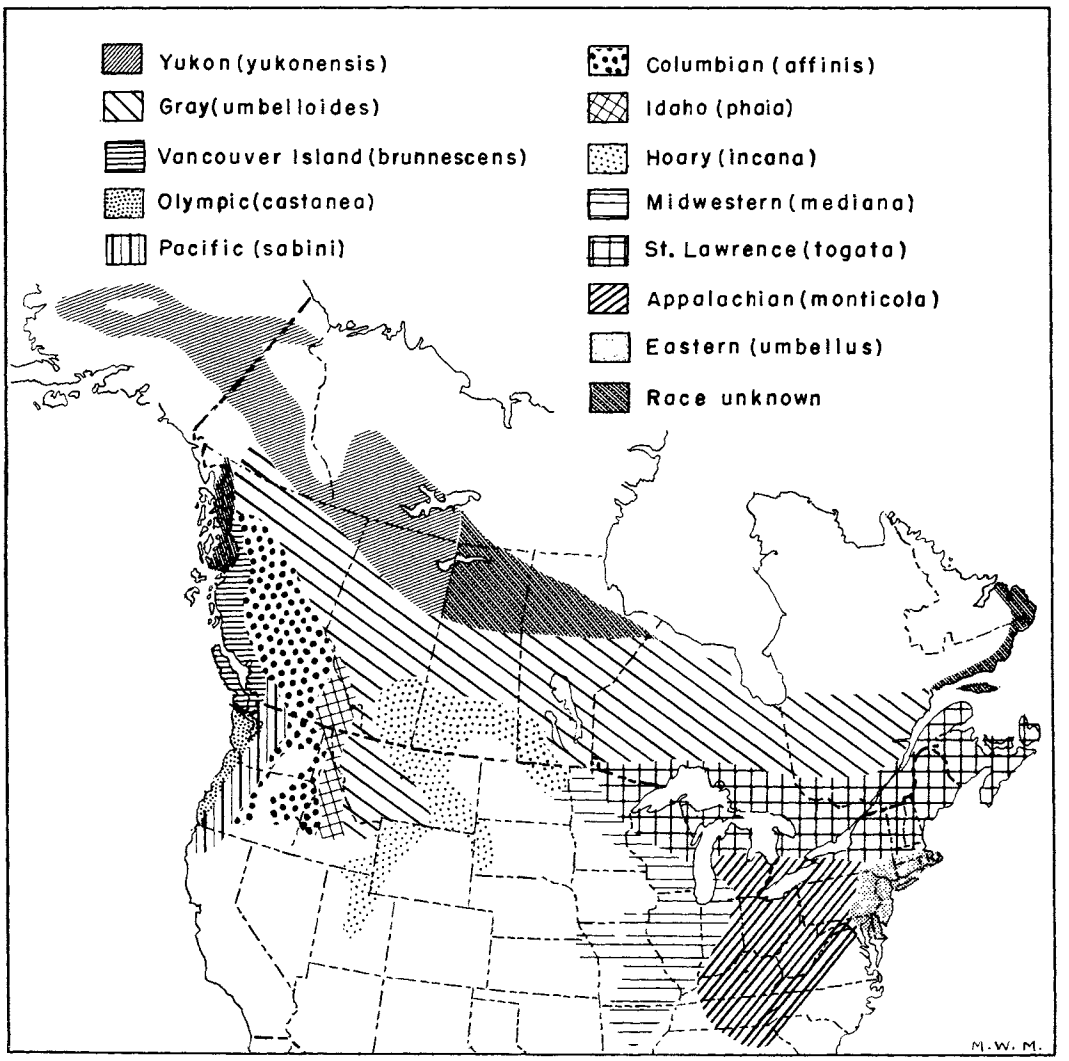


Fig. 4. Ruffed grouse (*Bonasa umbellus*), original distribution of subspecies.

land and aspen parkland areas, the Vancouver ruffed grouse (*B. u. brunnescens*) and the Olympic ruffed grouse (*B. u. castanea*) in the wettest sections of the Pacific rain forest, the Pacific ruffed grouse (*B. u. sabini*) in a slightly drier phase of this same climax type, and the Idaho ruffed grouse (*B. u. phaia*) in the drier disjunct of this type, known as the Columbian forest, in northern Idaho and southeastern British Columbia. The Columbian ruffed grouse (*B. u. affinis*) occupies the still drier habitats of the montane woodland area of interior British Columbia, Washington, and Oregon.

In the ruffed grouse, we find a classic example of the correlation of intensity of coloration with the amount of moisture in the environment, as well as with the density and background shades of the vege-

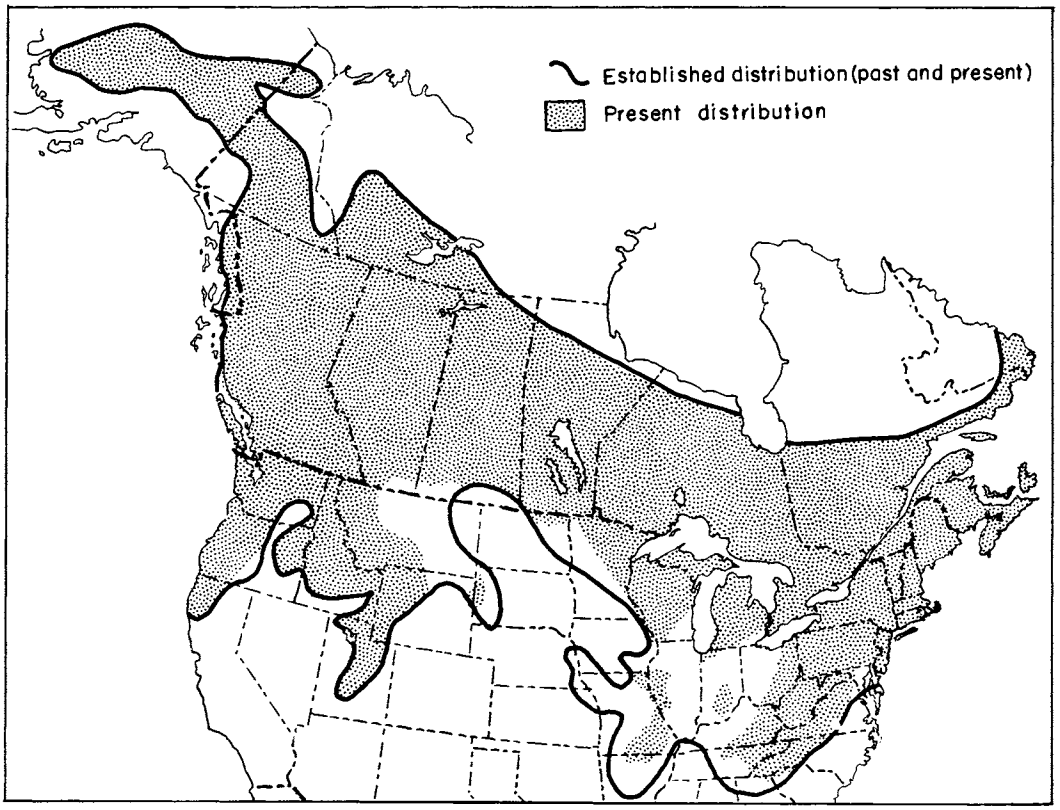


Fig. 5. Ruffed grouse (*Bonasa umbellus*), present distribution of subspecies.

tation cover, themselves correlated with moisture. Thus the darkest ruffed grouse are in the lush forests of the Olympic peninsula rain forest and the palest in the relatively arid aspen groves of the Great Basin mountains of Utah and the low hills rising out of the shortgrass prairies of the central states and provinces. The range of the ruffed grouse has receded considerably along its southern border (Fig. 5), largely because of man's interference with forest habitat. This is particularly true in the oak–savannah and grassland areas (Fig. 1), where woody growth has been eliminated extensively for agricultural purposes. On the other hand, second growths after fires and lumbering have benefitted ruffed grouse in many areas by interspersion and by turning forest succession back to younger stages (Hamerstrom and Hamerstrom 1961:286).

The two species of prairie chickens are birds of the climax grasslands, both the open, shortgrass prairies and the mixed tallgrass and woodland of the oak–savannah area (Fig. 6). The greater prairie chickens (*Tympanuchus cupido pinnatus*), most characteristic of the climax grassland, oak–savannah, and aspen parkland, have moved to some extent into the man-made grasslands within the naturally forested area of northern Minnesota, Wisconsin, Michigan, and southern Ontario. One race, the extinct eastern prairie chicken or heath hen (*T. c. cupido*), survived, before elimination by man, in what were

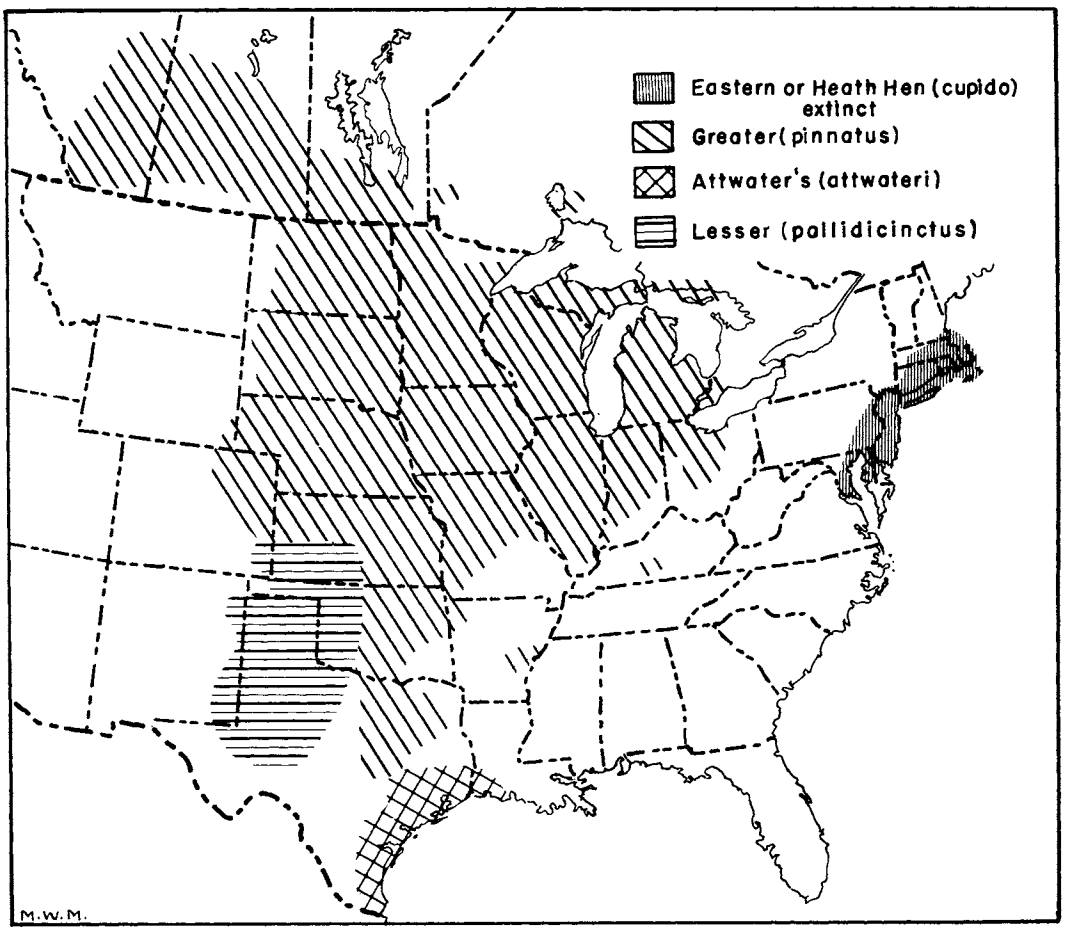


Fig. 6. Greater prairie chicken (*Tympanuchus cupido*) and Lesser prairie chicken (*T. pallidicinctus*), original distribution of species and subspecies.

probably fire-created "prairies" or blueberry barrens in the sandy soils along the northern Atlantic seaboard. Another subspecies, the Attwater's prairie chicken (*T. c. attwateri*) of the Gulf Coast prairies, seems about to follow its Atlantic-coast cousin to extinction because of the trend toward eliminating its natural grassland habitat.

The lesser prairie chicken (*T. pallidicinctus*) occupies the southwestern end of the grassland area. This area is characterized by a considerable amount of dwarf oak brush, on which the bird seems to depend. Although formerly geographically continuous but not overlapping in range with the greater prairie chicken, the lesser prairie chicken appears to have sufficiently separated morphological characters to be considered a distinct species by most ornithologists.

The ranges of both greater and lesser prairie chickens have been drastically reduced, largely because the original natural grassland habitats have been eliminated (Fig. 7). Both species now occur only locally throughout their formerly extensive ranges.

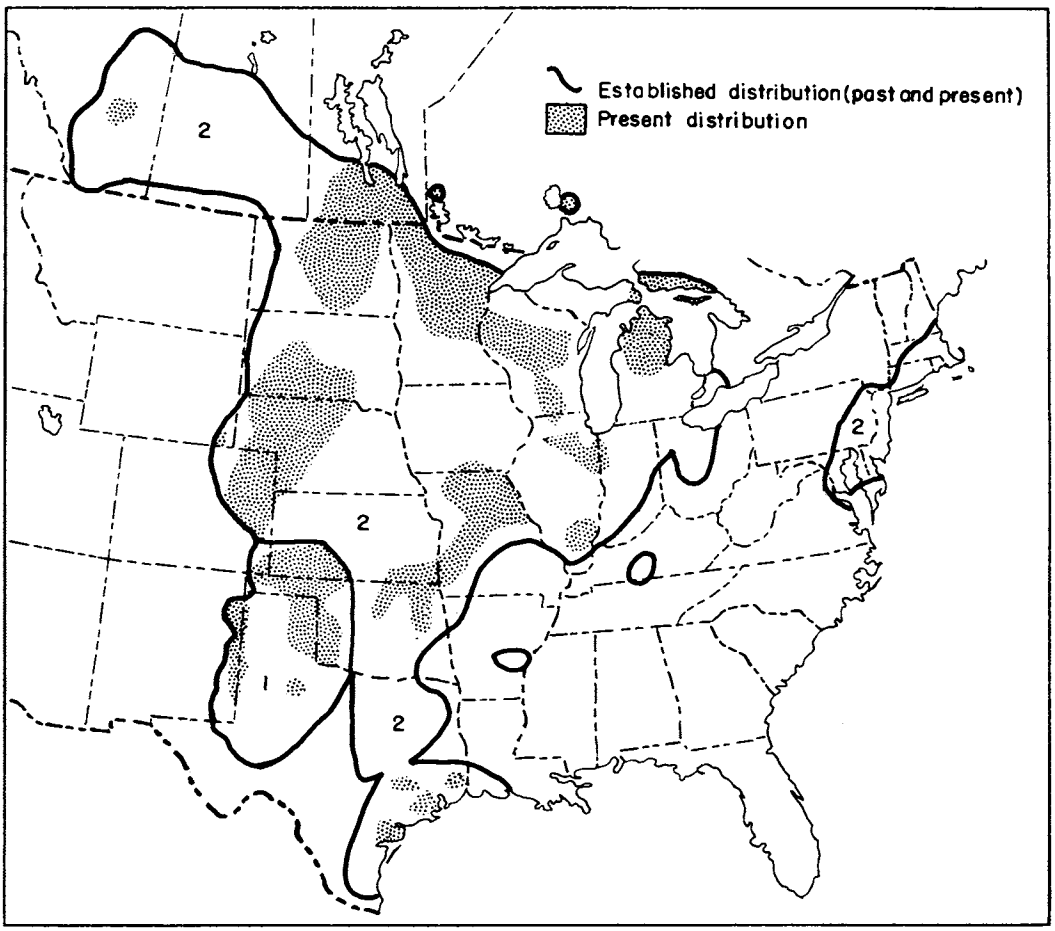


Fig. 7. Present distribution of species. 1—Lesser prairie chicken (*Tympanuchus pallidicinctus*). 2—Greater prairie chicken (*Tympanuchus cupido*).

The sharp-tailed grouse (*Pedioecetes phasianellus*) occupies brushy habitats in northwestern United States and western Canada (Fig. 8). These habitats include the climax sagebrush of the northern desert scrub area, occupied by the Columbian sharp-tailed grouse (*P. p. columbianus*); subclimax brush in the grasslands area and Rocky Mountain parks, occupied by the plains sharp-tailed grouse (*P. p. jamesi*); and the oak–savannah and lumbered and burned eastern deciduous and northern hardwood–conifer areas farther east, occupied by the prairie sharp-tailed grouse (*P. p. campestris*). Where there are extensive brushy openings in both the open and closed boreal forest areas, sharp-tailed grouse of several races occur: for example, the northern sharp-tailed grouse (*P. p. phasianellus*) in the Hudson Bay lowlands open boreal area and the Alaska sharp-tailed grouse (*P. p. caurus*) in both open and closed boreal areas of northern Alberta through northeastern British Columbia and Yukon Territory through the Yukon River valley of Alaska. Another boreal forest race (*P. p. kennicotti*) appears to be restricted to the vicinity of the Mackenzie

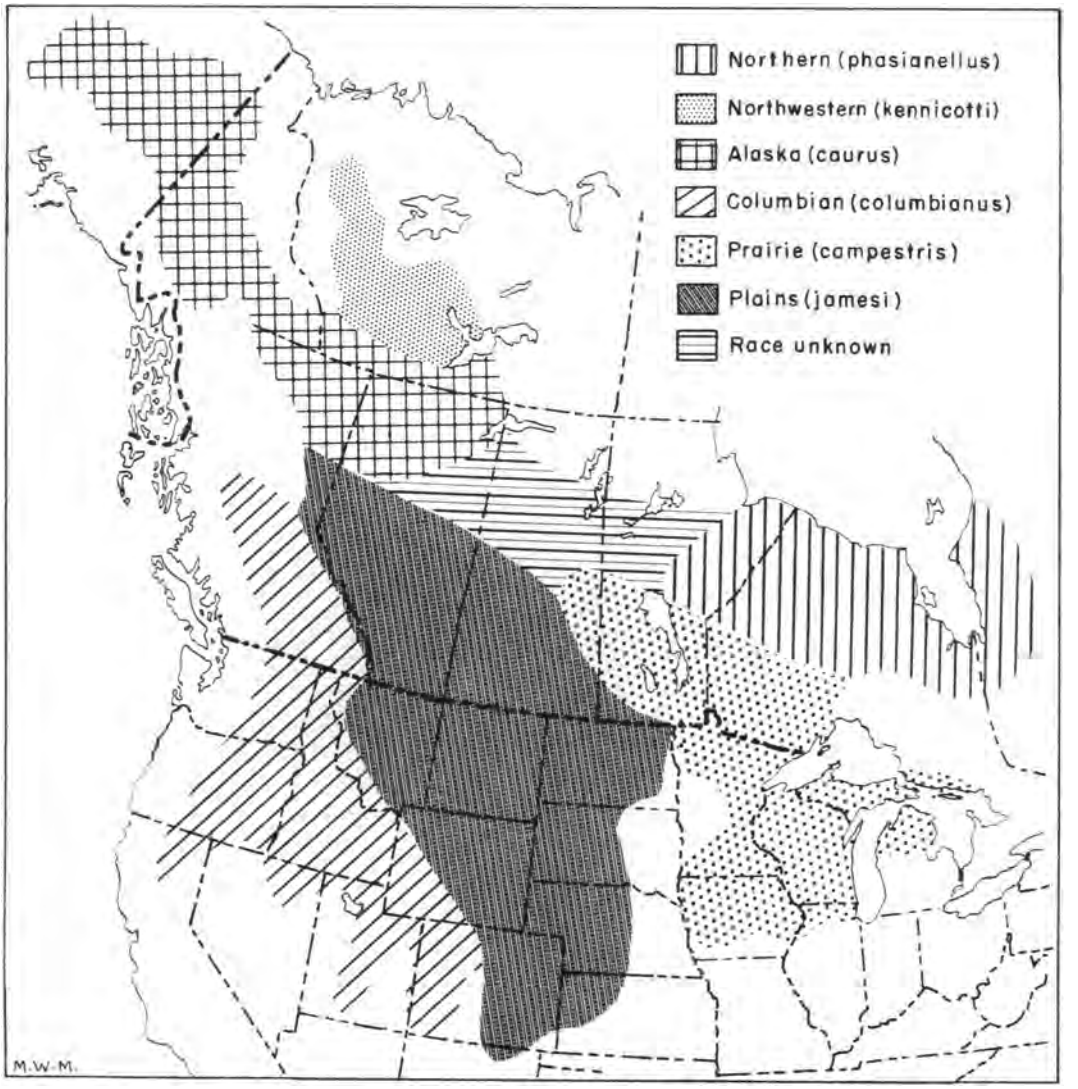


Fig. 8. Sharp-tailed grouse (*Pedioecetes phasianellus*), original distribution of subspecies.

River valley northwest of Great Slave Lake. The racial affinity of the sharp-tailed grouse which are known to occur in the predominantly closed boreal forest area across middle Alberta, Saskatchewan, and Manitoba is unknown because specimens from that extensive territory are lacking. The range of the sharp-tailed grouse has been greatly reduced (Fig. 9) from its former extent along its entire southern border, largely because its brushy habitat has been altered by agricultural practices.

The sage grouse is, in habitat, one of the most limited of the entire family. Mature growths of sagebrush appear to be necessary for its welfare, so its distribution is limited to areas where this type of growth occurs (Fig. 10). These are found primarily in the northern desert scrub area, where sagebrush is the climax dominant,

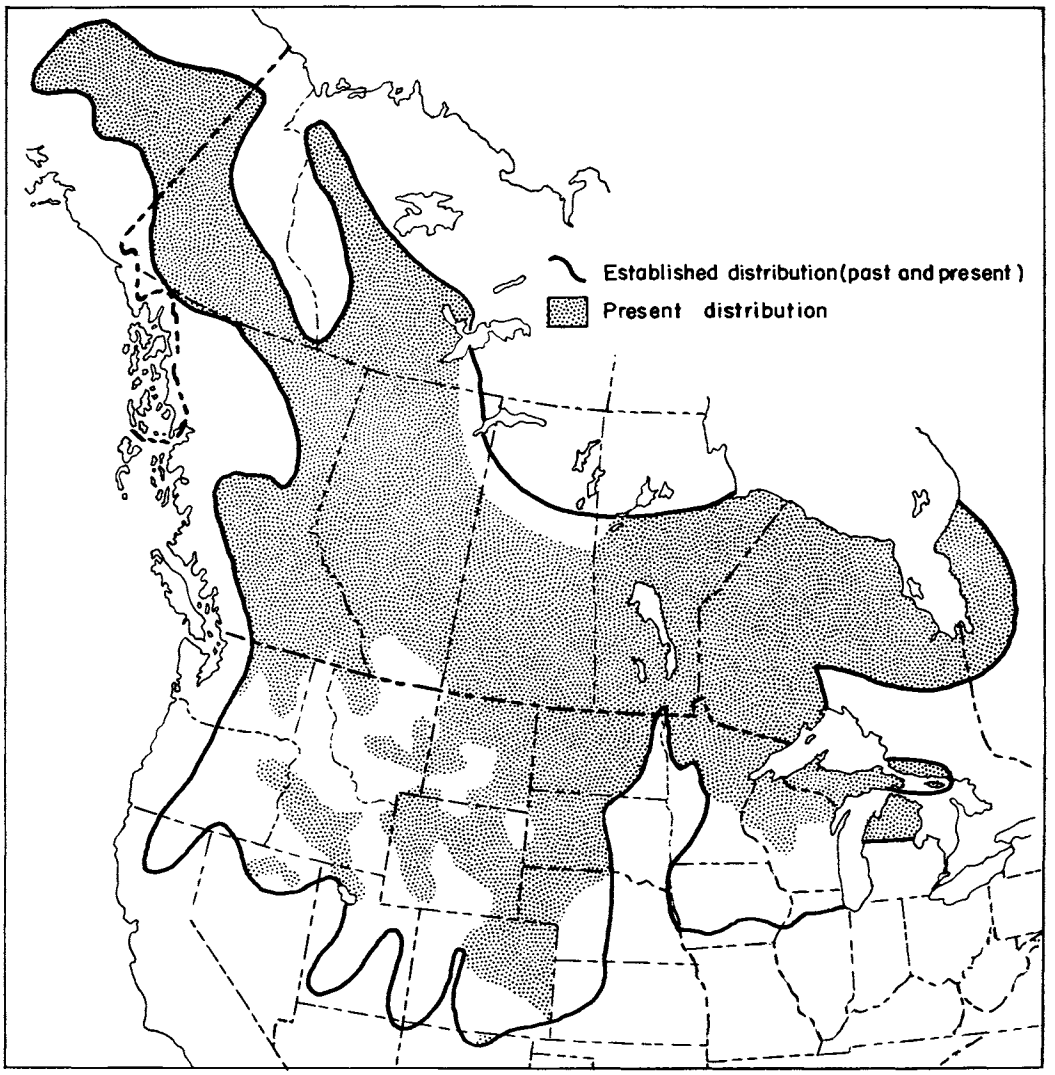


Fig. 9. Sharp-tailed grouse (*Pedioecetes phasianellus*), present distribution of subspecies.

and in the shortgrass plains and mountain parks, where it is subclimax after fire and overgrazing. Over much of the vast area, only one subspecies, the eastern sage grouse (*Centrocercus u. urophasianus*), occurs. But in the northern horn of the Great Basin and its extension, the Columbia Basin of eastern Oregon and Washington, the western sage grouse (*C. u. phaios*) is found. The population which occurs in the Sierra Nevada of California, like that of northwestern Nevada, appears to be intermediate between these two races. The sage grouse occupies most of its former range, although greatly reduced by sagebrush elimination practices in some areas; it has disappeared only from scattered areas along the periphery (Fig. 11).

The white-tailed ptarmigan (*Lagopus leucurus*) is the representative of this cir-

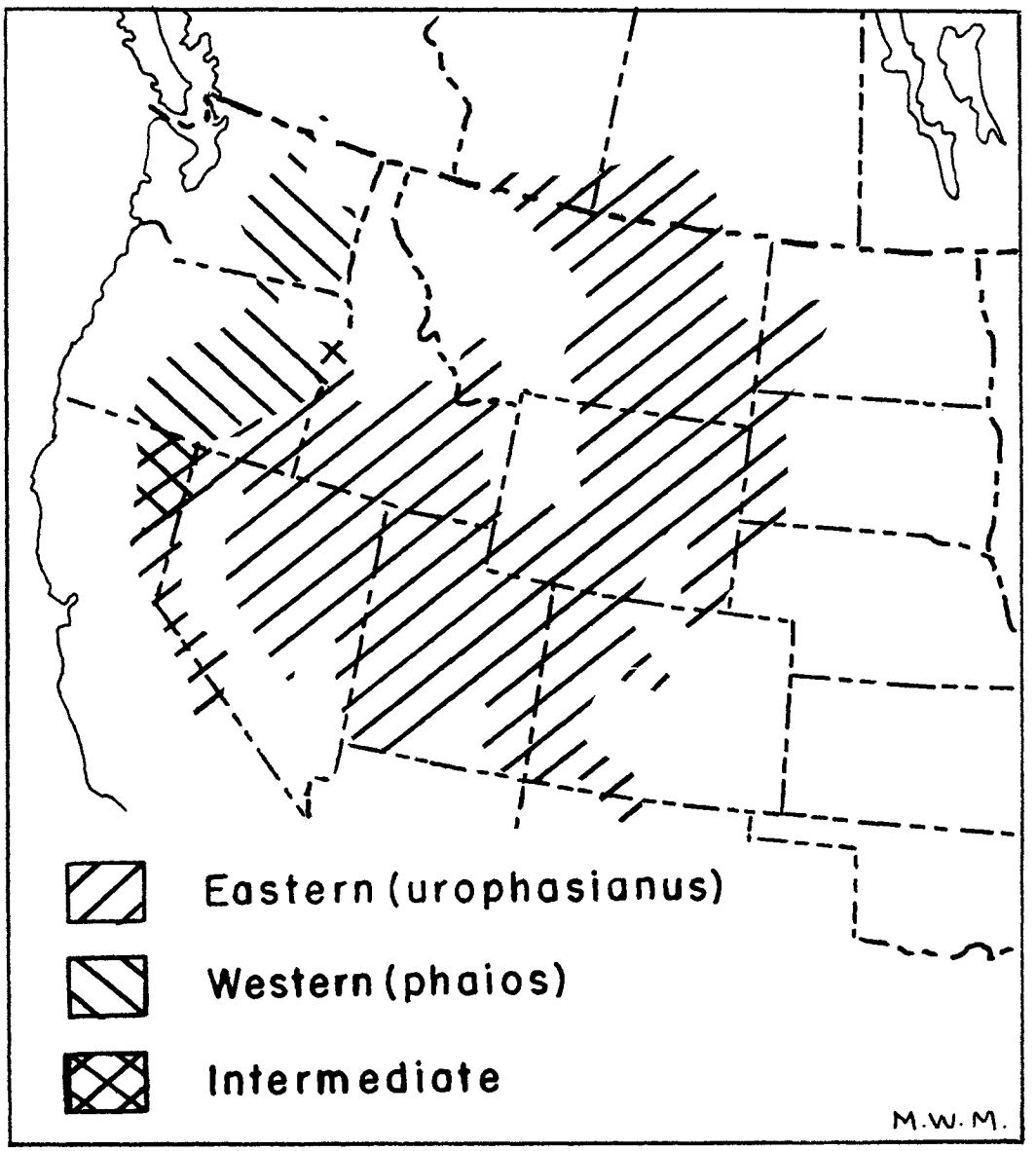


Fig. 10. Sage grouse (*Centrocercus urophasianus*), original distribution of subspecies.

cumpolar genus of arctic grouse which occupies alpine meadows in the arctic–alpine area of the mountains of southern Alaska and Yukon Territory southward through the mountains of western Canada and United States to New Mexico (Fig. 12). The insular nature of the arctic–alpine habitats in the southern part of the mountains has interrupted gene flow, with the result that several races have evolved there: the Vancouver white-tailed ptarmigan (*L. l. saxatilis*) of Vancouver Island; the Rainier white-tailed ptarmigan (*L. l. rainierensis*) of the Cascade Mountains of Washington,

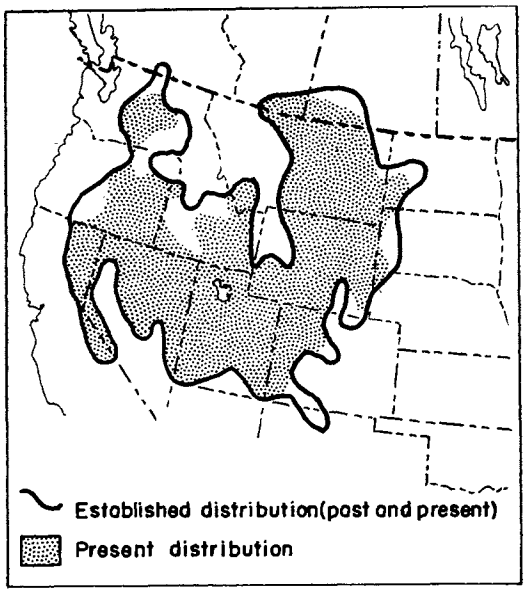


Fig. 11. Sage grouse (*Centrocercus urophasianus*), present distribution of species.

and the southern white-tailed ptarmigan (*L. l. altipetens*) of Wyoming, Colorado, and New Mexico. The continuous nature of the alpine tundra farther north has discouraged racial differentiation, with the result that one subspecies, the northern white-tailed ptarmigan (*L. l. leucurus*), extends from Montana all the way north to northern Yukon Territory. An offshoot population in the Alaska Range and adjoining coastal mountains of Alaska has differentiated into a fifth subspecies, the Kenai white-tailed ptarmigan (*L. l. peninsularis*). In view of the great similarity of the various environments throughout the range of this alpine grouse, it would appear that racial differentiation has resulted primarily from geographical isolation rather than from natural selection of adaptive characters.

Throughout most of its range, the arctic–alpine habitat of this species has not been exploited by man to any important degree, nor has this bird been hunted to any extent. However, grazing of alpine meadows may have seriously reduced or even eliminated white-tailed ptarmigan populations in such places as Washington, western Montana, and northern New Mexico (Hamerstrom and Hamerstrom 1961:285).

The willow ptarmigan (*Lagopus lagopus*) is circumpolar in distribution, except in Greenland and Iceland, chiefly beyond treeline. It occurs to some extent in the tundralike openings of the open boreal area. It also extends southward for some distance in the alpine zone of both North American and Eurasian mountain ranges. The habitat of the willow ptarmigan is low scrub, such as dwarf willow and birch, in the moist portions of the arctic and alpine tundras.

In North America, the willow ptarmigan varies geographically to some extent (Fig. 13). This variation is, for the most part, without obvious ecological correlation, and thus, presumably, is the result of geographical separation. However, Alexander's willow ptarmigan (*L. l. alexandrae*), of the humid North Pacific coastal mountains of Alaska, is sharply differentiated from the Canada willow ptarmigan (*L. l. albus*) and the Alaska willow ptarmigan (*L. l. alascensis*) of interior regions. This pattern of geographical variation occurs in a number of other species in various habitats in these same areas. Also, the differentiation between the Aleutian Islands, Shumigan Islands, Kodiak Island, and Newfoundland populations and those of the adjoining mainland is a familiar pattern followed by numerous other species of birds. The distinction between the Canada and the Ungava (*L. l. ungavas*) subspecies is probably due to physical separation by Hudson Bay. The differentiation between the northern willow ptarmigan (*L. l. leucopterus*) of the Arctic islands and a few northern extremities of the mainland, and the more south-

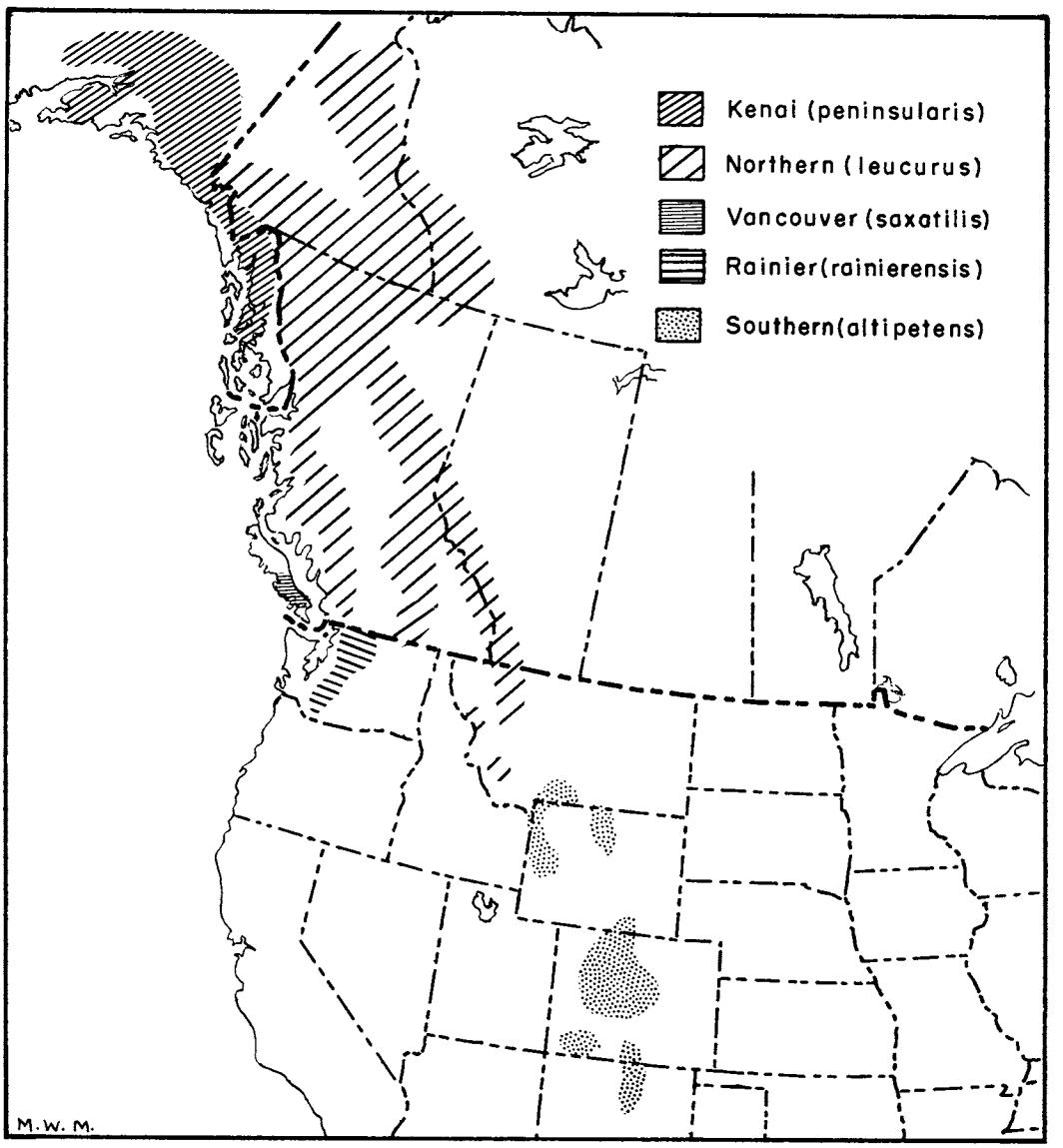


Fig. 12. White-tailed ptarmigan (*Lagopus leucurus*), original distribution of subspecies.

erly Canada and Ungava races suggests a possible climatic or other environmental correlation.

The map for this species is based on breeding distribution. Willow ptarmigans are known to be irregularly migratory and frequently show up considerable distances south of their breeding range. Inasmuch as the arctic–alpine tundra habitat has been changed relatively little in historic times, it is probable that, despite periodic changes caused by violent fluctuations in Arctic weather, the distribution of the willow ptarmigan has been relatively unchanged during this period.

The rock ptarmigan (*Lagopus mutus*)

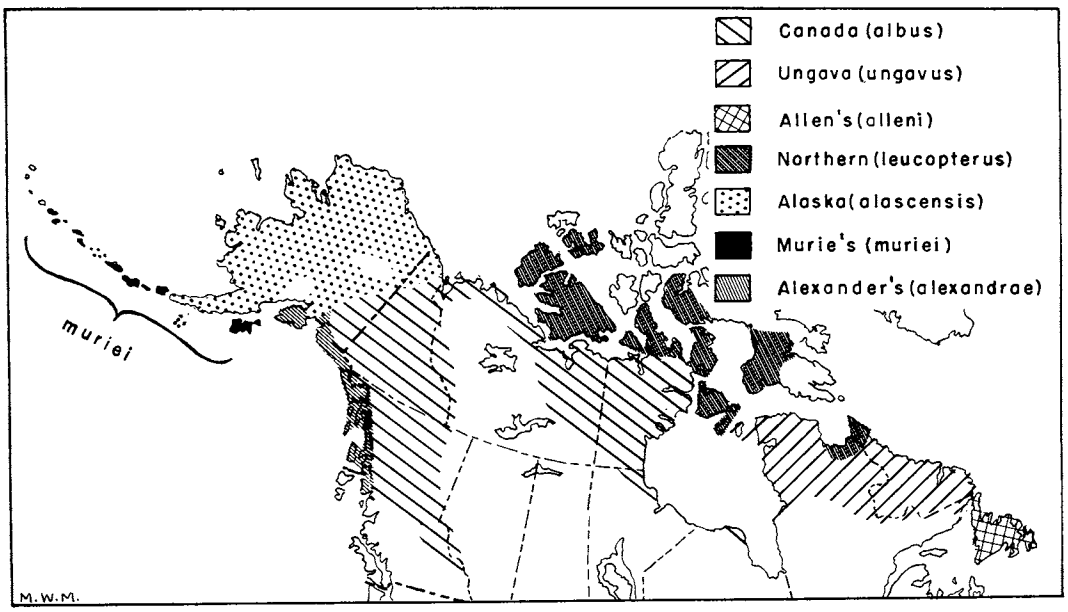


Fig. 13. Willow ptarmigan (*Lagopus lagopus*), original distribution of subspecies.

is completely circumpolar in the arctic–alpine areas along the northern fringe of both New and Old World continents and southward for considerable distances in the higher mountains (Fig. 14).

As its name implies, the rock ptarmigan chooses the rocky arctic–alpine barrens for its breeding area, as distinct from the less sparsely vegetated habitats of the other two North American species of this genus. This choice of habitat appears to have resulted in a somewhat more northerly, as well as a wider, distribution of the rock ptarmigan than of its close relatives. In North America and Greenland, there is considerable geographical variation in rock ptarmigans. This is particularly marked in the Aleutian Islands, where six subspecies have been differentiated. In a species having as little cover afforded by habitat as the rock ptarmigan, it might be expected that concealing coloration of plumage would be essential for survival, and thus background-matching colors in the plumage would be selected for especially, in race formation through natural selection. Thus, the color of the rocks and lichen flora might be expected to be correlated with such racial variation in plumage color as occurs in this species. Physical isolation also undoubtedly plays an important role in a species which ranges over such vast areas.

The rock ptarmigan is irregularly migratory and occurs in winter at considerable distances south of its breeding range. Because there is little human settlement in the inhospitable regions occupied by this species, it is probable that very little change in its distribution has taken place in recent times.

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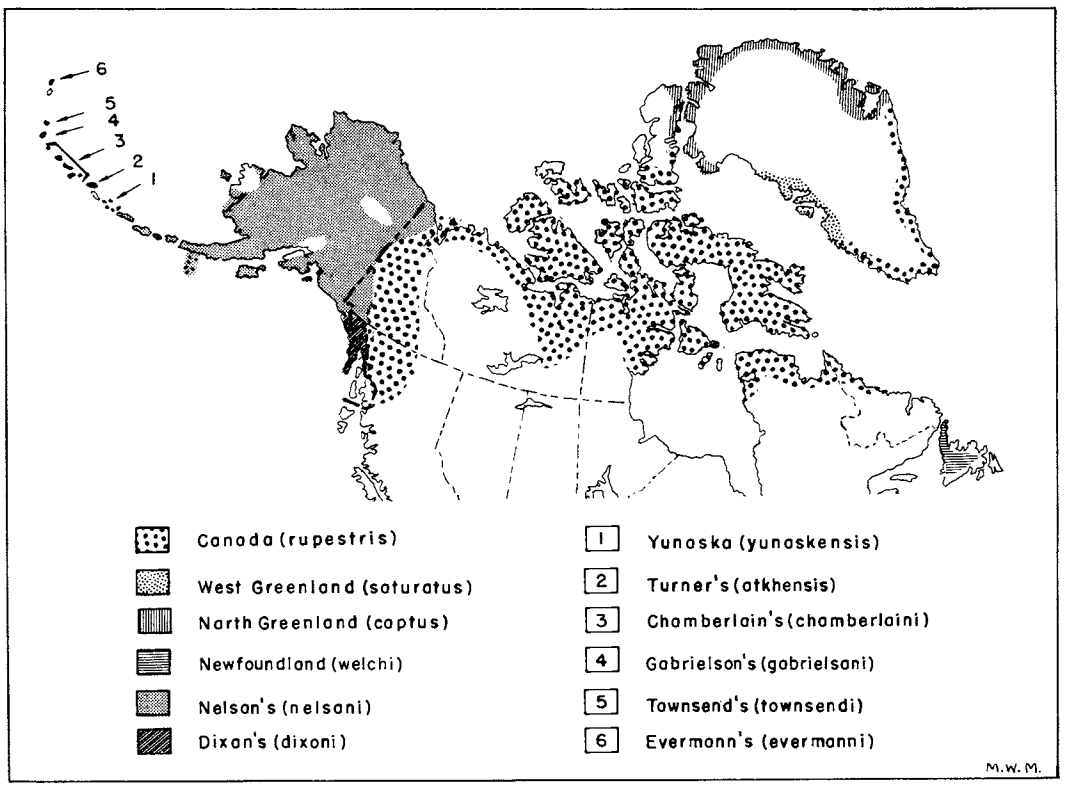

Fig. 14. Rock ptarmigan (*Lagopus mutus*), original distribution of subspecies.

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