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A REVISION OF THE RUFFED GROUSE

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There has long been need of a comprehensive study of the geographical variation and taxonomy of the well known North American game bird, the Ruffed Grouse (*Bonasa umbellus*). The writers have at last amassed sufficient material in the United States National Museum, including the Biological Surveys collection of the United States Fish and Wildlife Service, together with specimens loaned by other museums and owners of private collections, to make this possible. In addition to the above, other specimens were examined in the Academy of Natural Sciences of Philadelphia. In all, the material used in this study consisted of 803 specimens assembled in Washington and a large number examined elsewhere. The material, therefore, has been far more ample than that available to any previous investigators.

For first-hand information on the habitat of ruffed grouse acknowledgments are due to Stanley P. Young, Dr. H. H. T. Jackson, Frederick C. Lincoln, Major E. A. Goldman, Dr. Clarence Cottam, and William H. Marshall, all of the Fish and Wildlife Service, and Edward A. Preble, formerly of the old Bureau of Biological Survey; also to Dr. Alexander Wetmore and Dr. Remington Kellogg, of the United States National Museum. To Dr. Alden H. Miller we are indebted for information on the geographic variation of specimens of Ruffed Grouse from western North America in the Museum of Vertebrate Zoology. For the loan of important comparative material we wish to thank John T. Zimmer, of the American Museum of Natural History, James L. Peters, of the Museum of Comparative Zoology, H. B. Conover, of the Field Museum of Natural History, W. E. Clyde Todd, of the Carnegie Museum, Dr. Harry C. Oberholser, of the Cleveland Museum of Natural History, Dr. J. Van Tyne, of the Museum of Zoology of the University of Michigan, Dr. Robert T. Orr, of the California Academy of Sciences, Dr. George M. Sutton, of Cornell University, Woodrow Goodpaster, of the Cincinnati Museum of Natural History, A. M. Brooking, of the Hastings (Nebraska) Museum, A. M. Bailey, of the Colorado Museum of Natural History, Dr. W. H. Headlee, of Purdue University, Dr. D. Eldon Beck, of Brigham Young University, Dr. Angus M. Woodbury, of the University of Utah, M. Dale Arvey, of Boise Junior College, and C. O. Handley, of the Virginia Cooperative Wildlife Research Unit, and Albert F. Ganier, Stanley G. Jewett, Dr. Louis B. Bishop, Dr. Ira N. Gabrielson, Frederick C. Lincoln, and Walter A. Weber, for specimens from their private collections.

PREVIOUS WORK

Tetrao umbellus and *Tetrao togata* were first described binomially by Linnaeus (1766:275), the former based on the Ruffed Heath-cock or Grouse of Edwards (1758:79, pl. 248), presumably from eastern Pennsylvania, and the latter based on La grosse Gelinote de Canada, *Bonasa major Canadensis*, of Brisson (1760:207), presumably from the region of Quebec City. W. E. C. Todd (1940:391) has fixed the type locality of *Tetrao togata* as Quebec City.

Stephens (1819:298) placed the above two forms, which he considered as one and the same, together with *Tetrao cupido* Linnaeus, in a separate genus, which he called

Bonasa. Subsequently Gray (1840:62) designated *Tetrao umbellus* as the type of this genus. Douglas (1829:137, 148) described two additional forms from western North America under the Linnaean genus *Tetrao*: *Tetrao umbelloides*, from the valleys of the Rocky Mountains, lat. 54° N., and near the sources of the Columbia River, east of the coast and Cascade ranges, and *Tetrao sabini*, from the coast of northwest America between the 40th and 49th parallels. Todd (1940:393) has further restricted the type locality of *umbelloides* to Henry House, Alberta, and Hall (1934:10) has set Vancouver, Washington, as the restricted type locality of *sabini*.

These four species were reduced to subspecific rank under *Bonasa umbellus* by the American Ornithologists' Union Committee on Classification and Nomenclature (1886:172-173). Stone (1907:198) renamed the genus of the Ruffed Grouse *Hylobrontes* on the basis of the "first species rule," which Stone thought would be adhered to rigidly by the Committee on Nomenclature. On this basis *Bonasa* would have been transferable to the Prairie Chicken, *Tetrao cupido*. However, subsequent action by the A.O.U. Committee upheld the use of *Bonasa* as the generic name for the Ruffed Grouse as designated by Gray (1840) and that is the genus under which the species has appeared in all editions of the A.O.U. Check-list.

The ruffed grouse of Nova Scotia and New Brunswick were separated and named *Bonasa umbellus thayeri* by Bangs (1912:378) with type locality at Digby, Nova Scotia, and Grinnell (1916:166) described *Bonasa umbellus yukonensis* from Forty-mile, Yukon Territory, on the Yukon River near the Alaska boundary. Other forms that have been proposed are: *Bonasa Jobsii* Jaycox (1871:182) based on birds from Ithaca, New York, and *Bonasa umbellus helmei* H. H. Bailey (1941:1) with type locality at Miller Place, Long Island, New York.

In the most thoroughgoing revision of the species to date, which, however, was confined to eastern North America, Todd (1940) described three additional races: *monticola*, from Cheat Bridge, West Virginia; *canescens*, from Abitibi River, Ontario; and *medianus*, from the Minneapolis region, Minnesota.

H. B. Conover (1935) studied the dark brown *sabini* complex of the Pacific Coast, and separated the Vancouver Island bird, which he called *brunnescens*. At the same time he noted differences in populations from the Olympic Peninsula and from central southern British Columbia, which the present writers are recognizing as separate subspecies. Leonard Uttal (1941:74) studied the geographic variation in the extent of tarsal feathering in ruffed grouse and found significant differences: northern birds in general have the tarsal feathering extending farther down toward the toes than populations from farther south. He suggested that taxonomic revision of the birds, on the basis of this character, might be illuminating. It might be added here that Mr. Uttal has gone over our series with us in connection with the present study and has given us the benefit of his ideas based on a large number of measurements pertaining to the tarsus.

In the most recent systematic treatment of the species, Hellmayr and Conover (1942:214) have followed virtually the racial differentiation set forth in the fourth edition of the A.O.U. Check-list (1931) with the exception of the inclusion of *brunnescens*, from Vancouver Island. Footnote mention was made of Todd's three new races from the eastern part of the continent, *medianus*, *monticola*, and *canescens*, which had been described too late for more thorough consideration.

INDIVIDUAL AND GEOGRAPHICAL VARIATION

Few species of birds are more variable than the Ruffed Grouse. This variability is in part individual, but to a marked degree it has a geographical or racial significance also.

As is well known, ruffed grouse have two more or less well defined color types, the "brown and gray phases," usually indicated by a brown or gray tail, but exhibiting every imaginable intermediate condition. There is also the brown-ruffed condition which may or may not be correlated with tail color. Furthermore there is a well marked size difference between the two sexes, particularly in the tail.

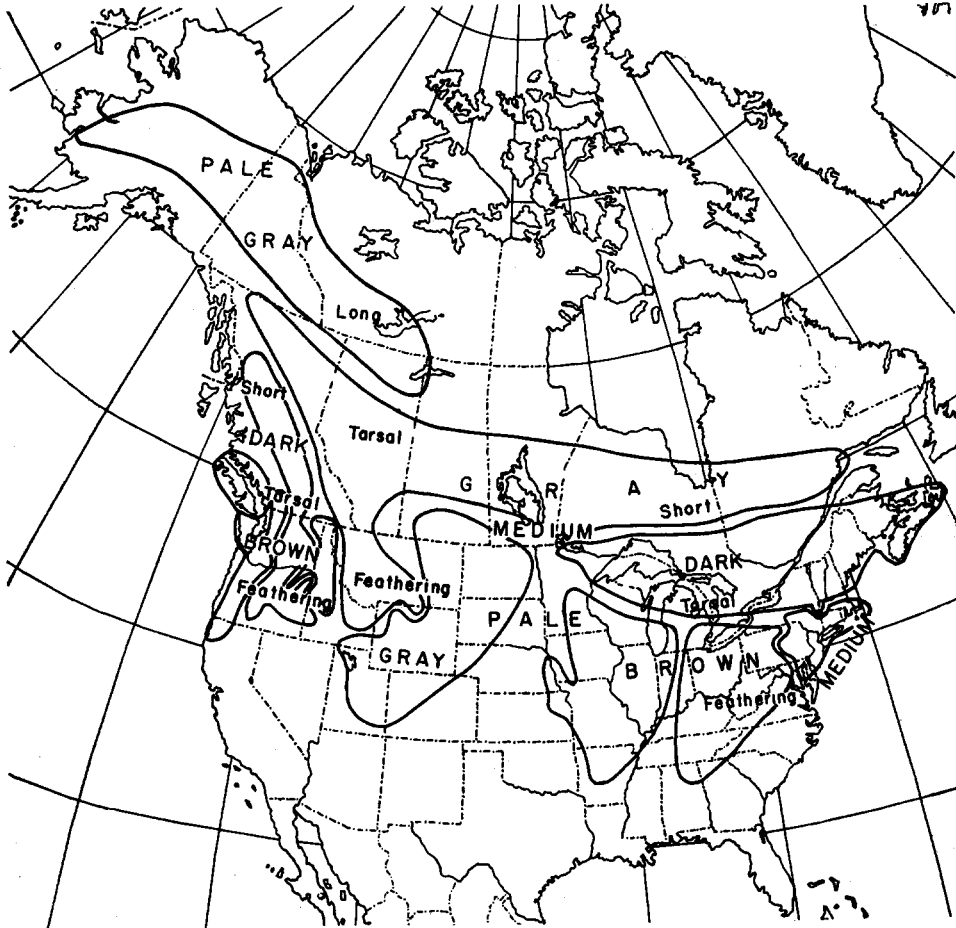


Fig. 26. Distribution of major characters subject to geographical variation in the Ruffed Grouse. The two main color characters, predominantly brown or predominantly gray, modified as dark, medium, and pale, are designated by capitals. Amount of tarsal feathering is indicated in capital and lower case letters; "Short Tarsal Feathering," for example, means a greater proportion of tarsus is unfeathered. Solid lines indicate limits of recognized races.

Unfortunately for previous students of the group, who had to work with material geographically less complete and locally less ample than ours, it so happens that unusually large numbers of specimens from intermediate areas (between the ranges of two or more races) have been collected and have tended to obscure the true characters in an apparently meaningless welter of individual variation. This is especially true of such areas as southern New England, central New York, southern Michigan, the southern portions of the Prairie Provinces and southern British Columbia. With adequate series laid out geographically, these otherwise troublesome specimens quickly assume

their correct place and even substantiate by their intermediacy the validity of the characters of the adjacent forms.

Taking into consideration the very great individual variation over the entire range of the species, several well marked clines or trends in geographic variation are noticeable. Generally speaking brownish hues prevail on the two coasts, while grayish tones replace them in the interior and to the north. Other clines are found in the relative darkness and pallor of the pigmentation and in the proportion of the tarsus covered by feathers. Tarsal feathering reaches its maximum extent in Alaska, and decreases in amount to the southward. The difference is even more pronounced in progressing both to the east and to the west of the Rocky Mountain region. Size is a good criterion in separating the two sexes, the male usually being considerably larger, particularly in tail length. Neither dimensions nor proportions, however, seem to have any significant geographical variation. In fact the average measurements of ruffed grouse throughout the length and breadth of their range are remarkably constant. There are slight geographical trends in average size measurements, but these are probably never significant in distinguishing any race from its nearest neighbor. On the average eastern birds are slightly larger than those from western localities, in wing and tail, but in toe and tarsal measurements the largest are rather conspicuously centered among the dark brown Pacific Coast birds.

ECOLOGICAL SIGNIFICANCE OF VARIATION

One of the most gratifying facts about the geographical variation of ruffed grouse is its obvious correlation with ecological factors. Each of the major biotic communities or biomes of the North American Upper Austral, Transition, Canadian, and Hudsonian life-zones, with the exception of the Grassland Biome, has at least one recognizable race of *Bonasa* which seems to be characteristic of it. (For further discussion of the correlation of bird distribution with biomes the reader is referred to Pitelka, 1941.) In some instances individual races or subspecies are confined to a single association, or region, having the same climax dominants throughout, within the biome. The Ruffed Grouse, probably because of its dependence upon the buds of deciduous trees for winter food, is predominantly a deciduous-forest bird. For this reason it is only within the region of the Deciduous Forest Biome, in the Upper Austral Life-zone of the eastern United States, that this species can be considered as characteristic of the climax community. Even here, however, it is probably more abundant on the borders of the climax forest or in subclimax woodlands. In the Canadian and Transition life-zones of the mountains and the Pacific Coast region of the western part of the continent, where coniferous trees are the climax dominants, the Ruffed Grouse is confined almost entirely to the subclimax communities usually dominated by species of poplar, birch, willow, or alder.

Whereas the northern limit of the distribution of the Ruffed Grouse seems to coincide with the northern limit of biotic communities dominated by vegetation of tree size, the southern limit does not. Deciduous forest growths seemingly suitable for supporting populations of these birds occur south of the range of *Bonasa umbellus*. Some other force, possibly the combined effect of high summer temperatures, atmospheric moisture, and forest cover, is the limiting one here.

Although the life form of dominant vegetation seems to be the chief agent limiting the distribution of the species as a whole, racial variation seems to be correlated to a large extent with atmospheric moisture. For this reason it also appears to be correlated with the distribution of different climax community types, which, in turn, are limited largely by precipitation and humidity. Roughly speaking the greatest intensity of brown coloration is found in the Atlantic and Pacific coastal regions, where rainfall and

humidity are relatively high, particularly in the misty southern Appalachian Mountains and in the fog-drenched coast of Washington. The gray tones on the other hand are most pronounced in the relatively arid Rocky Mountain and Great Plains regions. More northern latitude also seems to produce a graying effect, indicating that temperature as well as moisture may be correlated with color variation. Thus grouse from both Alaska and northern Canada are much more grayish than populations from equally near the coast farther south. Of course the intensity of light in the habitat is an agent which might operate in this case. Indeed this may be the direct force controlling the color variation in all instances. Unfortunately there are few exact data available relative to this factor within the actual habitats in which grouse occur. Still less information, based on controlled experiments concerning the morphological effects of any environmental factor on birds, is available. It would seem to be a stimulating field for experimentation that has been grossly neglected, and that needs the attention of investigators with access to facilities for carrying on extensive breeding experiments with wild birds under controlled environmental conditions. The difficulties are obvious, but the significance of the possible results certainly warrants the attempt.

An attempt is made in the statements of the distribution of races to give the descriptions of ranges in terms of distribution in ecological communities as well as in geographical areas. To avoid confusion as to what is intended by certain controversial ecological terms and concepts the following explanation is offered. Unlike some of his colleagues the senior author thinks that it is possible to bring together the life-zone concept of Merriam and the biome concept of more recent ecologists (see Pitelka, 1941), and to unify the nomenclature, using the older life-zone names where applicable. Thus "biomes" would replace "faunas" as subdivisions of life-zones, and the geographical boundaries of the zones, instead of being based on isotherms, would be delimited by the more fluid boundaries of their component biomes. It should be noted that in the present paper the concept of the Transition Life-zone is somewhat different from that of Merriam and his followers (1910); it includes the ecotones between the northern conifer and subalpine forests on the one hand and the deciduous forests and grassland on the other. The present concept of the Transition Life-zone, therefore, encompasses the various forest climax communities and their respective developmental stages that have been called "Lake Forest," "Pine-Hemlock-Northern Hardwood Forest," and the various "Montane Forests," and the "Aspen Parklands." The *biome* is the largest biotic community possible with a uniform type of life form presented by its primary climax dominant species in response to a certain set of climatic conditions and with some similarities in species composition throughout. The *association* is used here in the broad sense as a subdivision of a biome in which the climax community contains the same species as primary dominants throughout. The various seral or developmental stages (associations) leading up to the climax are characteristic of and are included in the "Association."

KEY TO RACES OF *BONASA UMBELLUS*

- a. General coloration more brownish than grayish.
 - b. Dark brown, ventral barring pronounced.
 - c. General coloration very dark (chestnut to dark auburn).
 - d. General coloration distinctly brownish with little or no grayish cast.
 - e. Very reddish, back bright argus brown to dark chestnut, tail auburn to bay.....*B. u. castaneus*
 - ee. Duller and less reddish, back between Prout's brown and Dresden brown, tail dull ochraceous umber (brown phase).....*B. u. brunnescens*
 - dd. General coloration with more grayish or dusky appearance; tail argus brown to cinnamon brown.....*B. u. phaios* (brown phase)

- cc. General coloration lighter (sayal brown to argus brown).
 d. Distinctly brownish with little or no grayish cast.
 e. Ventral barring darker—cinnamon brown to dark mummy brown *B. u. sabini*
 ee. Ventral barring lighter—dusky Isabelline to buckthorn brown *B. u. monticola*
 dd. Browns mixed with some gray.
 e. Blackish areas of upper parts more pronounced; brown parts darker and less rufescent—cinnamon brown to dark Prout's brown..... *B. u. togata*
 ee. Blackish areas of upper parts less well developed; brown areas paler and more rufescent—mikado brown to snuff brown..... *B. u. affinis* (brown phase)
 bb. Light brown, barring less pronounced.
 c. General coloration darker, head and neck with little if any grayish suffusion, tail (brown phase) nearly hazel..... *B. u. umbellus*
 cc. General coloration paler, head and neck with pale grayish suffusion, tail (brown phase) nearly ochraceous tawny..... *B. u. medianus*
 aa. General coloration more grayish than brownish.
 b. Definitely gray with little or no brownish wash.
 c. Very pale (smoke gray to pale neutral gray).
 d. Tarsus unfeathered* for $\frac{1}{4}$ its length or less; more white in upper parts *B. u. yukonensis*
 dd. Tarsus unfeathered* for not less than $\frac{1}{2}$ its length; less white in upper parts..... *B. u. incanus*
 cc. Darker (mouse gray to light grayish olive)..... *B. u. phaios* (gray phase)
 bb. Gray mixed with considerable brown.
 c. Tarsus unfeathered* for more than $\frac{1}{2}$ its length..... *B. u. affinis* (gray phase)
 cc. Tarsus unfeathered* for less than $\frac{1}{2}$ its length..... *B. u. umbelloides*

* Point of insertion of feathers on outside of tarsus to junction of tarsus with middle toe is measurement for unfeathered tarsus.

DESCRIPTIONS OF RACES

Bonasa umbellus umbellus (Linnaeus)

Eastern Ruffed Grouse

Tetrao umbellus Linnaeus (1766:275); based on The Ruffed Heath-cock or Grous, Edwards (1758:248); in Pennsylvania = eastern Pennsylvania.

Bonasa Jobsti Jaycox (1871:182); Ithaca, New York.

Bonasa umbellus helmei H. H. Bailey (1941:1); Miller Place, Long Island, New York.

Adult male (brown phase).—Feathers of forehead, crown, and occiput sayal brown to cinnamon brown, barred with blackish, and tipped with smoke gray to pale smoke gray; elongated crest feathers with blackish extended toward base on outer edges of both webs, leaving brown as a broad basal shaft stripe with lateral branches, the blackish marks very narrowly edged on their distal margins with cinnamon brown; nape sayal brown to cinnamon brown, tipped with smoke gray; interscapulars similarly brownish, but with smoke gray confined to the distal portion of shaft and a large terminal shaft spot, the remaining part of feathers irregularly crossed by blackish marks which fail to connect toward shaft; outermost of these marks often very broad (8-10 mm.); neck ruffs either deep black with slight bluish purplish sheen, dark fuscous black with blue-black tips to feathers, or bright auburn with narrow fuscous tips to feathers; upper back, lower back, and rump cinnamon brown to dark Brussels brown, the feathers of upper back with cordate terminal shaft spots of tillou buff to vinaceous buff, narrowly edged with black and occasionally sparsely flecked with blackish; feathers of lower back and rump with these spots broader, more oval and with a distally converging "V" of blackish within the light area, the spots separated from the tips of the feathers by 3 to 8 mm. of dark smoke gray; in rump feathers, brown areas faintly and sparsely vermiculated with blackish on concealed basal portions; upper tail coverts cinnamon brown, very broadly tipped with smoke gray (about 15 mm. wide) and crossed by 5 or 6 narrow, equally spaced, wavy fuscous black bands, each of which (except most distal one, which borders on proximal edge of gray terminal area) is followed distally by narrow band (wider than black band) of cinnamon buff to pale tawny olive, which in turn is followed by broken line of fine blackish dots; gray tips finely speckled or vermiculated with black, with large blotch of dark fuscous black, edged with auburn, in their middle portion.

Lesser and median upper wing coverts sayal brown to cinnamon brown, very narrowly and incompletely edged with blackish and with mesial streaks of pale buffy white, narrowly edged with dusky; greater upper secondary coverts similar, but with brown areas faintly vermiculated with blackish; greater upper primary coverts fuscous, externally narrowly edged with cinnamon brown, the edging widest basally; primaries fuscous on inner webs and terminally on outer ones, most of outer webs cartridge buffy to buffy white, with 5 to 7 dusky fuscous triangular bars, the base of each is against the shaft and its apex is at outer edge of vane, causing whitish areas to appear like reversed triangles; these dusky marks become small and faint or disappear entirely on distal third of feathers; secondaries fuscous, externally broadly edged with sayal brown, coarsely vermiculated with fuscous, and tipped with drab; the innermost secondaries have their inner webs also margined with vermiculated sayal brown with a wash of drab; scapulars like greater secondary coverts, but with light mesial streaks much wider and adjacent part of inner web extensively blackish.

Rectrices cinnamon to clay color, tipped broadly with smoke gray, with fine black vermiculations, subterminally broadly banded with fuscous black to bister, this band sometimes breaking down to a series of vermiculations in median pair of rectrices (possibly in younger adult birds); subterminal dark band edged basally with another smoke gray band similar to terminal one, remainder of feathers crossed by 7 to 9 narrow, wavy fuscous black bands, each followed distally by band of cinnamon buff, which, in turn, is edged distally by broken series of blackish vermiculations that extend in reduced size into the brown interspaces.

Loral stripe pale pinkish buff narrowly edged with blackish spots; lower eyelid a line of pinkish buff and black spots; feathers of cheeks and auriculars elongated, sayal brown, with blackish edges and pale ashy brown shaft streaks; chin whitish washed with buffy or pale ochraceous buff, the feathers sometimes tipped narrowly with black; throat light ochraceous buff, becoming whitish laterally on upper throat, the feathers forming the lateral and posterior portions of gular area tipped with fuscous black, producing a somewhat scalloped pattern; upper breast cinnamon brown to light auburn, each feather broadly tipped with smoke gray, so that in fresh plumage the brown is largely obscured; brown areas of feathers basally largely light pinkish cinnamon with darker cinnamon brown forming incomplete bands, especially subterminally; lower breast and upper and lateral parts of abdomen grayish white to pale smoke gray, subterminally crossed by broad bands of wood brown to buffy brown, narrowly edged on both sides with darker and the feathers washed with buff basally; brownish subterminal bands usually largely hidden by grayish white tips of feathers, especially on abdomen, these bands darker and more exposed on lateral feathers; middle of abdomen with no brown, pure grayish white; feathers of sides sayal brown to Saccardo's umber, slightly vermiculated with blackish and with white shaft streaks that expand distally into broad terminal spots; flanks similar, but brown areas more ashy and more vermiculated, the vermiculations forming narrow bands, the shaft streaks washed with grayish and not expanding into terminal spots; thighs drab to whitish, washed with pale vinaceous buff; under tail coverts clay color to cinnamon buff, broadly tipped with white, the white sometimes extending back in a narrow streak along shaft, the brown parts frequently with a few blackish spots; under wing coverts sayal brown to Saccardo's umber, with whitish mesial streaks; axillars white, banded broadly with sayal brown; iris hazel; bill dark brown; feet dark grayish olive with brownish wash.

Adult male (gray phase).—Similar to red phase except that interscapulars, back, lower back, and rump feathers and upper wing coverts have brown areas vermiculated and irregularly banded with smoke gray, the feathers completely margined with the same; in upper tail coverts and rectrices rufescent replaced by smoke gray, which is generally somewhat more abundantly flecked and vermiculated with black than in red phase; subterminal band is usually fuscous to fuscous black, but occasionally dark argus brown (in which examples the ruffs are usually auburn with blackish tips); outer margins of greater upper primary coverts paler—wood brown; sides, flanks, and thighs more ashy, and brown on under tail coverts reduced largely to narrow, incomplete cross bars. In the winter, grouse of both sexes differ from summer birds in the presence of "snowshoes" caused by the growth of the lateral scales on the toes, and also in the more extensive grayish tips and margins to the feathers which wear off by spring, giving a slightly more rufescent appearance to spring and summer specimens.

Adult female (both phases).—Similar to corresponding males but averaging smaller, particularly in the tail, and with shorter ruffs, the gray-phase females less pure gray on tail, more mixed or washed with rufescent than in gray males, and pectoral area in both phases more extensively tawny or hazel; cordate spots on feathers of back and rump smaller than in males and also more washed with avelaneous to wood brown.

Immature (both sexes).—Similar to adults of corresponding sex and phase, but ruffs slightly duller and slightly smaller; birds in this stage may be recognized however chiefly by the fact that they carry two outer primaries of the juvenal plumage which differ from the adult feathers in that their outer webs are not cartridge buff or whitish, marked with sayal brown, but pale fuscous, mottled and

stippled with pinkish buff to pale cinnamon buff. In the literature one finds statements to the effect that the juvenal primaries, such as are retained in the immature plumage, are light vinaceous cinnamon unmarked except for a very fine sprinkling of a slightly darker shade, but the difference between them and adult primaries is confined to their outer webs.

Juvenile (sexes alike).—Similar to adult female but browner above, more abundantly marked with sayal brown to Saccardo's umber on underparts, but these marks more irregularly disposed, not so clearly forming bars, but something between bars and heavy transverse mottling; tail feathers lacking heavy black subterminal band and smoke gray tips poorly developed; narrow blackish rectrices (about as in the adults in number) each followed distally by a band of pale sayal brown or cinnamon, lighter than rest of the feather, or by a band of pale smoke gray (possibly birds that would become gray-phased later on); head very different from adult—forehead, crown, and occiput snuff brown to Saccardo's umber, spotted with fuscous black; buffy whitish line extends from loreal antæ through both eyelids to sides of occiput; cheeks and auriculars snuff brown to Saccardo's umber, the former spotted with dusky sepia to fuscous black; chin and most of upper throat whitish, unmarked; feathers of back and rump and upper tail coverts different from those of adult—ashy sayal brown narrowly barred with sepia to fuscous; iris hazel brown; bill "brown and slate"; feet bluish white.

Downy young.—Forehead, crown, occiput, and nape pale ochraceous tawny, darkening medially and posteriorly to tawny, and paling laterally to light ochraceous buff on sides of crown and occiput, and on lores, cheeks, and auriculars; middorsal area from nape to tail bright russet, this area widening very considerably on lower back, the body down on either side of this ochraceous buff, becoming lighter ventrally; entire underparts ivory yellow to light cream buff, a fuscous black line extending from posterior end of eye to posterolateral angle of occiput; upper surface of wings pale russet, under surface cream buff.

Measurements (extremes and averages in millimeters): *Adult male.*—Wing, 174-190 (183.6); tail, 144-174 (159.0); culmen from base, 25.8-29.0 (27.0); tarsus, 41.9-47.9 (43.9); middle toe without claw, 32.4-39.0 (36.7); unfeathered part of tarsus, 21.7-31.1 (26.3); 20 specimens from Massachusetts, Rhode Island, eastern Pennsylvania, and southeastern New York. *Adult female.*—Wing, 170-188 (176.4); tail, 123-141 (132.6); culmen from base, 23.8-28.1 (26.3); tarsus, 39.6-43.6 (41.2); middle toe without claw, 32.7-36.9 (34.2); unfeathered part of tarsus, 20.2-30.0 (24.9); 16 specimens from Massachusetts, southeastern New York, and District of Columbia.

Distribution.—Climax and subclimax deciduous woodland of the Atlantic coastal White Oak-Pitch Pine Association and the northeastern portion of the Red Oak-Beech-Tulip Association in the Eastern Deciduous Forest Biome, Upper Austral and Lower Transition life-zones; extends north to central eastern and central Massachusetts, east-central and central New York, west to central New York and east-central Pennsylvania and south to Cape May, New Jersey, and, formerly, to Washington, D. C.

There is abundant evidence in the specimens at hand to show that *Bonasa umbellus monticola* ranges up through middle Pennsylvania to the northeastern part of that state. For this reason it would seem essential to restrict the type locality of *Bonasa umbellus umbellus*, which has always been given as merely "eastern Pennsylvania," to the vicinity of Philadelphia, in the southeastern part of the state. A specimen in the Academy of Natural Sciences of Philadelphia, from near-by Bryn Mawr, is typical of the paler bird that we are considering as *umbellus*. The Eastern Ruffed Grouse intergrades with *monticola* in south central New York, east central Pennsylvania, central Maryland, and northeastern Virginia. Specimens from the vicinity of Ithaca, New York, are somewhat intermediate toward *monticola*, but are nearer *umbellus*, thus making *jobsii* Jaycox a synonym of *umbellus*. Specimens from Long Island, New York, are intermediate between *umbellus* and *togata*, but like specimens from southern New England they average nearer *umbellus*, of which race *helmei* H. H. Bailey therefore becomes a synonym.

Bonasa umbellus medianus Todd

Midwestern Ruffed Grouse

Bonasa umbellus medianus Todd (1940:394); Excelsior, Minnesota. (?) *Bonasa ceres* Shufeldt (1913:300); Pleistocene of fissure beds of Arkansas). This name is proposed as either a *Bonasa* or a *Lagopus*; a critical study of the bones on which it is based is yet to be made. Even if it were proved to be definitely *Bonasa umbellus*, the name would not be available for the present subspecies, as there is no proof that the grouse of the Pleistocene and of the present day are subspecifically identical.

Adult.—Closely similar to the corresponding sexes and phases of *Bonasa umbellus umbellus*, but very slightly paler, the top and sides of head and neck with a pale grayish suffusion; on the average, breast less extensively washed with brownish, abdomen more albescent, and, in brown phase, tail paler, nearly ochraceous tawny (in brown phase of *umbellus* it is nearly hazel).

Juvenile.—No specimens seen.

Downy young.—No specimens seen.

Measurements: Adult male.—Wing, 174-185 (178.9); tail, 140-163 (150.6); culmen from base, 25.2-30.6 (27.8); tarsus, 41.8-45.8 (43.5); middle toe without claw, 34.5-39.5 (36.8); unfeathered part of tarsus, 18.4-30.2 (23.8); 19 specimens from southern Minnesota, Wisconsin, southwestern Michigan, and Iowa. *Adult female.*—Wing, 171-183 (176.6); tail, 127-159 (141.3); culmen from base, 26.0-28.2 (27.3); tarsus, 40.8-44.8 (42.7); middle toe without claw, 34.5-37.4 (35.4); unfeathered part of tarsus, 21.6-30.0 (25.4); 3 specimens from southern Minnesota and Illinois.

Distribution.—Climax and subclimax deciduous woodland of the White Oak-Shagbark Hickory Association in the Eastern Deciduous Forest Biome, Upper Austral Life-zone; ranges from southwestern Michigan, southern Wisconsin, and east-central Minnesota (Elk River), south, east of the Great Plains grassland, to central Arkansas (Hot Springs). To the east *Bonasa umbellus medianus*

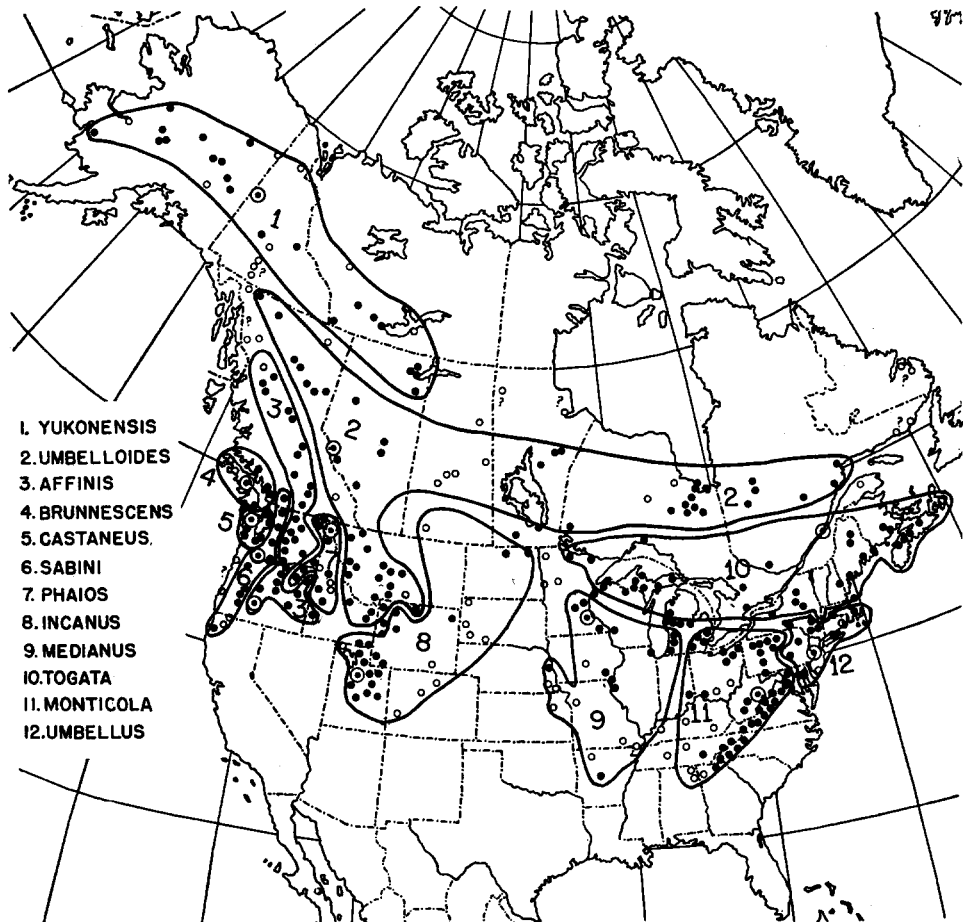


Fig. 27. Distribution of the races of the Ruffed Grouse (*Bonasa umbellus*). Solid black spots indicate localities from which one or more specimens have been examined by the authors. Open circles mark localities from which ruffed grouse have been recorded but from which no specimens have been examined by the authors. Type localities are shown by encircled dots.

Note.—The boundary lines on this map are designed to show the limits of racial characters which should not be confused with the limits of occurrence of ruffed grouse. There are large areas included within the boundaries of some races where no ruffed grouse occur at all, or, if they do, only in relatively small isolated islands of favorable habitat. This is particularly true of the regions in which forest communities intergrade with tundra or grassland.

intergrades with *Bonasa umbellus monticola* over a broad area in southern Michigan, Indiana, and probably formerly in western Kentucky and Tennessee.

Note.—If this race were not separated geographically from *Bonasa umbellus umbellus* by *Bonasa umbellus monticola*, its recognition might be questioned. There seems to us to be less difference between *medianus* and *umbellus* than between any other two subspecies of ruffed grouse herein recognized as distinct.

Bonasa umbellus monticola Todd

Appalachian Ruffed Grouse

Bonasa umbellus monticola Todd (1940:392); 2½ miles east of Cheat Bridge, Randolph County, West Virginia, 4,000 feet elevation.

Adult (brown phase).—Similar to that of *Bonasa umbellus umbellus*, but general coloration darker, under parts more regularly and more heavily barred and more strongly suffused with buffy; upper parts more brownish, less rufescent—Prout's brown instead of cinnamon brown as in *umbellus*; ventral bars become dark (dark sepia to clove brown) on flanks.

Adult (gray phase).—Similar to that of *Bonasa umbellus umbellus*, but upper and lower back darker, more brownish, the tail apparently never so pure gray, but always with at least a slight tinge of rufous; ventral bars darker, as in brown phase, but under parts less washed with buff. This plumage is very much like that of the brown phase of *togata*.

Juvenile.—There seem to be two phases in juveniles, both, as far as available material shows, possess brown tails, but one is much grayer above than the other. In the browner of the two phases, juveniles are like *Bonasa umbellus umbellus*, but darker, browner, less rufescent above, the blackish marks on the upper parts larger and the ventral barrings darker as in the adult. In the grayer of the two phases the areas of the nape, interscapulars, upper wing coverts, back, rump, and upper tail coverts that are Dresden brown to Saccardo's umber in the brown phase are wood brown, the pale areas of the interscapulars are pinkish buff (as opposed to cinnamon buff to pale clay color in the browner phase), and the ventral barrings are darker and less rufescent—buffy brown to sepia.

Downy young.—Similar to that of *Bonasa umbellus umbellus* but darker and more brownish, less vinaceous.

Measurements: Adult male.—Wing, 172-196 (186.8); tail, 139-181 (160); culmen from base, 24.4-31 (27.4); tarsus, 40-48.2 (44.5); middle toe without claw, 32.8-40 (36.5); unfeathered part of tarsus, 21.4-34.5 (28.5); 39 specimens from Virginia, West Virginia, North Carolina, Georgia, Maryland, western Pennsylvania, Tennessee, Ohio, and southeastern Michigan. *Adult female.*—Wing, 166-190 (178.6); tail, 121-156 (134.8); culmen from base, 23.8-29.3 (26.6); tarsus, 37.4-45 (41.1); middle toe without claw, 32.2-39.6 (35.1); unfeathered part of tarsus, 19.4-33.6 (27.2); 35 specimens from Virginia, West Virginia, North Carolina, Georgia, Tennessee, western Pennsylvania, Maryland, Ohio, and southeastern Michigan.

Distribution.—Climax and subclimax deciduous forest communities of the Red Oak-Beech-Tulip Association in the Eastern Deciduous Forest Biome, Upper Austral Life-zone, and both the Montane and Subalpine forests (Eastern Hemlock-Yellow Birch, and Red Spruce-Fraser Fir associations of the Transition and Canadian life-zones, respectively) in the Appalachian Mountains; ranges north to northeastern Pennsylvania, northeastern Ohio, and southeastern Michigan; east to northeastern and south-central Pennsylvania, central Maryland, northeastern, central, and southwestern Virginia, southwestern North Carolina and northern Georgia; and south to northern Georgia and northeastern Alabama. The western limit of the range of this race is ill-defined because of the fact that the species has been extirpated over much of the Mississippi Valley region where it formerly occurred. *Bonasa umbellus monticola* intergrades with *medianus* in central southern Michigan, Indiana, and probably also formerly in western Kentucky and Tennessee. The height of expression of its characters is found among specimens from the mountains of the southern part of the Appalachian Range.

Bonasa umbellus sabini (Douglas)

Pacific Ruffed Grouse

Tetrao Sabini Douglas (1829:137); Coast of Northwest America, between the 40° and 49° parallels, from Cape Mendocino to Vancouver's Island; restricted type locality—the vicinity of Fort Vancouver, Clarke County, Washington, according to Hall (1934:10).

? *Tetrao Fusca* Ord (in Guthrie, 1815:317); based on Small Brown Pheasant (Lewis and Clark, 1814:182). This name is considered as not certainly identifiable. Coues (1874:394) relegates it, with a query, to the synonymy of *Canachites franklini*, although in his later "History of the Exped. under . . . Lewis and Clark" (3, 1893:872), he definitely identifies it as *Bonasa umbellus fuscus*, "the variety of the ruffed grouse commonly called *Bonasa umbellus sabinei*. . . ." (largely because of the mention of

the fact that the breast meat is white). Even if Coues's later action were to be followed we would be unable to place the name because of the absence of a sufficiently circumscribed locality and the possibility of its applying equally well to *sabini* or *affinis*.

Adult (brown phase).—Similar to that of *Bonasa umbellus umbellus*, but much more darkly and richly colored (darker and richer than *Bonasa umbellus monticola* also, although closer in appearance to that race than to any other); black markings above more extensive and conspicuous; areas which are sayal brown to cinnamon brown in *umbellus* are orange cinnamon, cinnamon rufous, or hazel, those that are cinnamon brown to dark Brussels brown in *umbellus* are bright dark amber brown to rufescent argus brown; rectrices bright amber brown; ventral barrings darker—dark Dresden brown, narrowly edged with fuscous, the lateral bars on sides and flanks darker still—mummy brown to clove brown; thighs darker—wood brown to avellaneous, tinged with cinnamon buff. There are two varieties of this phase agreeing in all respects, except the color of the breast; in one variety this area is blackish, the feathers narrowly tipped with whitish or tawny, whereas in the other there is no black, but the feathers are bright tawny, becoming mummy brown only basally.

Adult (gray phase).—Similar to brown phase, but with feathers of crown, occiput, and nape, tipped with smoke gray; those of upper and lower back, and rump, and upper tail coverts terminally edged with pale neutral gray, vermiculated with blackish; rectrices as in gray phase of *Bonasa umbellus umbellus*, but darker, more washed with wood brown.

Juvenile.—None seen.

Downy young.—Darker and more brownish than that of *umbellus*. Indistinguishable from *monticola*.

Measurements: Adult male.—Wing, 177-187 (182); tail, 142-159 (151.7); culmen from base, 25.8-28.1 (26.5); tarsus, 43.0-45.1 (44.1); middle toe without claw, 39.0-41.9 (40.1); unfeathered part of tarsus, 16-28.6 (22.8); 6 specimens from Washington and Oregon. *Adult female*.—Wing, 170-181 (174.3); tail, 124-137 (130.2); culmen from base, 24.9-28.4 (26.4); tarsus, 41.2-44.2 (43.0); middle toe without claw, 33-39 (36.5); unfeathered part of tarsus, 17.8-28.0 (22.3); 6 specimens from Washington, Oregon, and California.

Distribution.—Subclimax deciduous woodlands (alder, maple, and willow communities) of the Western Red Cedar-Western Hemlock Association in the Pacific Moist Forest Biome, Transition Life-zone; from southwestern British Columbia, exclusive of Vancouver Island and the immediate vicinity of the coast, southward west of the Cascade Range, through Washington and Oregon, exclusive of the Olympic Peninsula and the immediate vicinity of Puget Sound, to northwestern California (Humboldt Bay and Salmon River).

***Bonasa umbellus castaneus* new subspecies**

Olympic Ruffed Grouse

Type.—No. 157949, United States National Museum (Biol. Surv. Coll.); adult male (brown phase); Soleduck River, elevation 1,200 feet, Olympic Mountains, Washington; collected August 29, 1897, by Vernon Bailey; original number 439.

Adult (brown phase).—Darkest and most richly colored of all the predominantly brown races of the species, being even darker than *sabini* and more reddish than *brunnescens*; brown of upper parts deep chestnut to dark auburn with no grayish mixture; ventral barrings Dresden brown to raw umber, darkening to mummy brown on sides and flanks, the chin, throat, breast, and upper abdomen, sides, flanks, and under tail coverts heavily washed with ochraceous buff; ruff black or rufescent, black being the commoner of the two.

Adult (gray phase).—None seen.

Juvenile.—None seen.

Downy young.—Darker and more reddish and less buffy than in *Bonasa umbellus umbellus*.

Measurements: Adult male.—Wing, 176-187 (182.8); tail, 145-168 (153.9); culmen from base, 25.6-29.9 (27.8); tarsus, 43.6-48.0 (45.3); middle toe without claw, 38.9-42.2 (40.7); unfeathered part of tarsus, 16.0-29.4 (23.5); 11 specimens from the Olympic Peninsula and the Puget Sound region. *Adult female*.—Wing, 170-178 (174.9); tail, 130-139 (131.8); culmen from base, 23.6-28.0 (26.5); tarsus, 41.2-45.5 (44.0); middle toe without claw, 37.0-39.7 (38.6); unfeathered part of tarsus, 20.8-29 (24.6); 9 specimens from the Olympic Peninsula and the Puget Sound region.

Distribution.—Subclimax deciduous woodland (alder and willow communities) in the very wet portion of the Western Red Cedar-Western Hemlock Association, in the Pacific Moist Forest Biome, Transition Life-zone; Olympic Peninsula, and the immediate vicinity of the shores of Puget Sound in western Washington; ranges south to Fort Steilacoom, Cedarville, and Shoalwater Bay, possibly also farther south along the "fog forest" belt in Oregon, although no specimens have been seen from the coast south of the Columbia River to establish this as a fact.

Bonasa umbellus brunnescens Conover
Vancouver Island Ruffed Grouse

Bonasa umbellus brunnescens Conover (1935:204); Comox, Comox District, Vancouver Island, British Columbia.

Adult (brown phase).—Similar to that of *Bonasa umbellus umbellus*, but darker, more brownish, less rufescent; also darker, more brownish, than *sabini* and more brownish, less reddish, than *castaneus*; general color of upper parts between Prout's brown and Dresden brown, tail dull ochraceous umber; under parts heavily barred with grayish ochraceous umber and washed extensively with tawny buff.

Adult (gray phase).—Similar to brown phase but top of head, neck, back, rump, and upper tail coverts mixed and vermiculated with dark smoke gray; rectrices dark smoke gray, barred and vermiculated with black and without any brownish tinge (the heavy black wavy bars are usually single in this race in both phases, whereas in *sabini* and *castaneus* they are double with a pale ochraceous band in between them); under parts as in brown phase, but much less washed with buffy.

Juvenile.—Similar to that of *Bonasa umbellus umbellus*, but very much darker brown, with more blackish; also darker than juvenal *togata* and *monticola*; above cinnamon brown to Prout's brown, as opposed to sayal brown in *B. u. umbellus*; ventral barrings darker—dusky Dresden brown.

Downy young.—None seen.

Measurements: Adult male.—Wing, 179-189 (183.7); tail, 144-157 (148.6); culmen from base, 26.6-28.3 (27.6); tarsus, 44.0-46.8 (45.6); middle toe without claw, 40-41 (40.3); unfeathered part of tarsus, 24.7-29 (26.7); 6 specimens, including the type, from Vancouver Island, British Columbia. *Adult female*.—Wing, 173-181 (176.3); tail, 124-134 (128.4); culmen from base, 24.4-27.4 (26); tarsus, 41.8-45.2 (43.0); middle toe without claw, 37-39.9 (38.4); unfeathered part of tarsus, 20.5-28 (25.3); 6 specimens from Vancouver Island, British Columbia.

Distribution.—Subclimax woodland (alder, willow, and maple communities) of the Western Red Cedar-Western Hemlock Association in the Pacific Moist Forest Biome, Transition Life-zone; Vancouver Island, British Columbia, and the adjoining mainland from the vicinity of the city of Vancouver, British Columbia, north at least to Malaspina Inlet near Lund. There are no records for ruffed grouse on the coast of British Columbia between this locality and Port Simpson, near the Alaska line; it is doubtful if *brunnescens* ranges much farther north than the immediate vicinity of Vancouver Island.

Bonasa umbellus togata (Linnaeus)
St. Lawrence Ruffed Grouse

Tetrao togatus Linnaeus (1766:275); based on La grosse Gelinote de Canada, *Bonasa major Canadensis* Brisson (1760:207); in Canada = city of Quebec (*apud* Todd, 1940:391).

Bonasa umbellus thayeri Bangs (1912:378); Digby, Nova Scotia.

Adult (brown phase).—Similar to that of *Bonasa umbellus umbellus* but darker brown, less rufescent, above, the areas that are sayal brown to cinnamon brown in *umbellus* being Dresden brown to Prout's brown in *togata*, the parts that are Brussels brown in *B. u. umbellus* being similar but washed with raw umber; upper parts generally with a little more mixture of grayish and with blackish marks more extensive, the underparts similar but more heavily barred than in *umbellus*. In *B. u. umbellus* the brown phase is more frequent than the gray; in *Bonasa umbellus togata* the opposite is true.

Adult (gray phase).—Similar to that of *Bonasa umbellus umbellus* but darker, both in browns and grays of upper parts, the brown as in the brown phase of *togata*—Dresden brown to Prout's brown; blackish markings more extensive, the gray areas, including the tail, smoke gray, much more finely and abundantly vermiculated with blackish than in *umbellus*; underparts more heavily and abundantly barred than in *umbellus*.

Juvenile.—Darker and more grayish than that of *Bonasa umbellus umbellus*.

Downy young.—Darker and more grayish and less buffy than in *Bonasa umbellus umbellus*.

Measurements: Adult male.—Wing, 173-192 (181.5); tail, 142-174 (156.9); culmen from base, 22.8-29.2 (26.1); tarsus, 40.3-46.0 (42.7); middle toe without claw, 33.0-39.9 (35.9); unfeathered part of tarsus, 20.0-30.9 (25.2); 32 specimens from Ontario, Nova Scotia, New Brunswick, Maine, New Hampshire, northern Massachusetts, northern New York, northern Michigan, northern Wisconsin, and northern Minnesota. *Adult female*.—Wing, 168-184 (176.0); tail, 119-144 (130.6); culmen from base, 21.0-29.3 (25.2); tarsus, 36.8-44.0 (41.4); middle toe without claw, 31.3-36.7 (34.6); unfeathered part of tarsus, 20.0-28.0 (23.8); 21 specimens from Ontario, Quebec, Nova Scotia, New Brunswick, Maine, New Hampshire, northern New York, northern Michigan, and northern Wisconsin.

Distribution.—Subclimax deciduous woodland (birch and aspen communities) of the White Pine-Hemlock-Sugar Maple Association, which forms the ecotone between the Northern Conifer and the

Eastern Deciduous Forest biomes in the lower Canadian and upper Transition life-zones; ranges from northern New England and Nova Scotia (probably north to Cape Breton Island and the Gaspé Peninsula), westward across southern Quebec and southern Ontario (including the north shore of Lake Superior) to central northern Minnesota, south to northeastern Massachusetts (Manchester), east-central New York (Piseco), southeastern Ontario (Toronto), midway down the Lower Peninsula of Michigan (Midland County) and northern Wisconsin (Ashland County).

Specimens from Nova Scotia average slightly darker and more richly colored than typical *togata*, but the difference is so slight and the overlap is so great that it is not considered on the same plane with that which distinguishes other recognized races of ruffed grouse. Therefore *thayeri* Bangs may best be treated as a synonym of *togata*.

***Bonasa umbellus affinis* new subspecies**
Columbian Ruffed Grouse

Type.—No. 95021 United States National Museum; adult male (gray phase); Fort Klamath, Oregon; collected October 28, 1882, by Captain Charles Bendire; original number 254.

Adult (gray phase).—Similar to the corresponding phase of *Bonasa umbellus umbellus* but darker more brownish above, more heavily barred below (in its general appearance intermediate between the gray phase of *umbellus* and that of *sabini*); feathers of top of head more solidly blackish, edged with smoke gray, and basally pale ochraceous tawny on their hidden portions; interscapulars and inner upper wing coverts cinnamon brown with large blotches and some vermiculations of fuscous to black, and with pale shaft streaks of tilleul buff to pale smoke gray; feathers of upper back similar but with less blackish, more mottled with smoke gray on their terminal portions; feathers of lower back, and rump, and upper tail coverts Prout's brown, sparingly vermiculated with black, with broad, tear-shaped whitish shaft spots which are longitudinally streaked and edged narrowly with black, the feathers edged with smoke gray, the extent of the terminal gray increasing on upper tail coverts; rectrices darker gray than in *B. u. umbellus*—smoke gray to light grayish olive with faint ochraceous tinge, especially along shaft and on proximal edge of each of the black wavy bands; rectrices slightly more heavily vermiculated with black; below more heavily barred, the bars dusky Isabelline to tawny olive, darkening on sides and flanks to sepia and mummy brown; lower throat and upper breast more strongly washed with ochraceous tawny than in *umbellus* of same phase. The gray phase is commoner than the brown.

Adult (brown phase).—Similar to gray phase but tail sayal brown with cinnamon wash, instead of smoke gray, the upper parts of head and body and upper wing coverts browner, less grayish, more rufescent, but not as rufescent as the brown phase of *sabini*; pale shaft streaks of the interscapulars pale ochraceous tawny, the upper back and lateral brown areas of interscapulars Dresden brown to mikado brown, vermiculated with blackish; lower back and rump dark mikado brown to rufescent Prout's brown; ventral barrings darker than in gray phase—Dresden brown darkening on the sides and flanks to mummy brown. This phase is closest to the brown phase of *togata*, but has the black markings less extensive.

Juvenile.—Similar to that of *Bonasa umbellus umbellus* but very slightly more rufescent (more than in *monticola* also) above and with the ventral bars darker—sepia to mummy brown; rectrices and outer webs of secondaries bright ochraceous tawny.

Downy young.—None seen.

Measurements: Adult male.—Wing, 171-191 (181.7); tail, 130-170 (152.4); culmen from base, 23.4-28.8 (26.3); tarsus, 40.4-45.5 (42.9); middle toe without claw, 34.2-41.0 (37.6); unfeathered part of tarsus, 14.5-29.2 (21.6); 42 specimens from British Columbia, Washington, and Oregon. *Adult female*.—Wing, 170-185 (176.2); tail, 123-157 (132.4); culmen from base, 23.9-28.4 (26.2); tarsus, 36.0-42.2 (40.6); middle toe without claw, 32.5-39.3 (35.2); unfeathered part of tarsus, 14.0-25.0 (19.4); 16 specimens from British Columbia, Washington, Oregon, and Idaho.

This race, which has been identified by numerous authors as the far separated *togata*, probably is a composite subspecies comprising two or three distinguishable ecological races inhabiting areas of their respective habitats in scattered mountain regions. The range of variation within the populations included in *affinis* is greater than in any other subspecies. It includes very pale gray individuals similar to Utah birds, medium brownish gray examples similar to *umbelloides*, as well as the darker, more brownish, types considered as typical of the present subspecies. Certainly the ecological conditions embraced within the range of *affinis* are more diverse than those encountered by any other subspecies. However, the correlation of these character differences with the habitat differences is too poorly understood at present to distinguish them nomenclaturally. A more thorough study of the problem in the field, however, might show such recognition to be desirable on the basis of ecological segregation of the type mentioned by Miller (1942:34) in certain species of the San Francisco Bay region.

Distribution.—Subclimax deciduous woodlands (alder, aspen, poplar, birch, and willow communities) of the montane and lower subalpine forests in the Transition and Canadian life-zones; ranges from Fort Klamath and Harney, Oregon, northward east of the Cascades (excluding the mountains of northeastern Oregon, southeastern and northeastern Washington), through the interior of British Columbia, to Hazelton. Specimens from Bear Lake in north-central British Columbia and from Telegraph Creek farther to the northwest in the same province had best be considered as intermediate between *affinis* and *umbelloides*.

The range of *Bonasa umbellus affinis*, as here delineated, includes populations of much paler and more grayish birds (possibly representing a distinct "ecological race") from the more arid interior regions of Washington and Oregon. The extreme examples of this type are found among specimens from Tunk Mountain, Aeneas, Twisp, Mazama, Molson, and Oroville, in Okanogan County, and Swan Lake and Curlew in Ferry County, Washington.

Bonasa umbellus phaios new subspecies

Idaho Ruffed Grouse

Type.—No. 158052 United States National Museum (Biol. Surv. Coll.); adult male (gray phase); Priest River, Idaho; collected October 9, 1897, by R. T. Young; original number 324.

Adult (gray phase).—Similar to that of *Bonasa umbellus umbellus* but less brownish, more grayish, and much darker, the smoke gray of upper parts of latter being replaced by mouse gray to light grayish olive, abundantly and heavily vermiculated with black; general dorsal coloration more grayish than brownish, only interscapulars and upper surface of wings being brownish—Saccardo's umber to dusky olive brown and dull sepia (even the interscapulars largely grayish terminally); lower back and rump feathers basally and laterally sepia, but this color less extensive than vermiculated gray parts of feathers; below more heavily barred than *umbellus* (more like *affinis* and *togata*), the bars pale Saccardo's umber to mummy brown, the throat and breast strongly tinged with pale ochraceous tawny.

Adult (brown phase).—Similar to that of *Bonasa umbellus umbellus* but much darker, less rufescent, more brownish (more like corresponding phase of *brunnescens*, but with more grayish or dusky); tail Dresden brown tinged, especially laterally, with ochraceous tawny, the brown of upper parts of head, body, and wings dark, dull Saccardo's umber to dark Dresden brown, vermiculated with black, the feathers of the upper and lower back with a dark grayish mixture; feathers of rump darkened to Prout's brown, medially tipped with dark smoke gray to pale grayish olive; below similar to gray phase but slightly less buffy on breast.

Juvenile (male only seen).—Above much grayer than in *Bonasa umbellus umbellus*, the general coloration of upper parts of head, body, wings, and tail drab to ashy hair brown, the interscapulars, scapulars, and a few of feathers of back having ashy tilleul buff shaft stripes and cross bars with incomplete broad clove brown to blackish interspaces; outer margin of secondaries buffy avellaneous, lesser upper wing coverts with light brownish olive tinge; crown and occiput dark mouse gray, the feathers with broad black terminal areas, margined and narrowly tipped with dark mouse gray; hind neck, sides of neck and breast washed with ochraceous tawny; ventral barring mummy brown.

Downy young.—None seen.

Measurements: Adult male.—Wing, 175-193 (182.7); tail, 141-171 (157.7); culmen from base, 24.8-28.6 (26.6); tarsus, 39.8-46.0 (42.7); middle toe without claw, 34.8-39.7 (37.6); unfeathered part of tarsus, 15.7-28.8 (23.2); 34 specimens from Washington, Oregon, and Idaho. *Adult female.*—Wing, 173-182 (178.6); tail, 124-134 (130.2); culmen from base, 23.5-27.0 (25.2); tarsus, 39.6-43.4 (41.1); middle toe without claw, 34.4-37.5 (36.2); unfeathered part of tarsus, 20.9-27.0 (23.8); 10 specimens from Washington and Idaho.

Distribution.—Subclimax deciduous woodlands (aspen and willow communities) of the Idahoan Montane Forest (Western Larch-Western White Pine Association), Transition Zone; west slopes of Rocky Mountains in Idaho, west to southeastern and northeastern Washington and to northeastern Oregon, in the Blue Mountains. Possibly it extends farther north into southeastern British Columbia, but no specimens have been seen to establish this fact. Specimens from the Boise National Forest in southwest central Idaho are intermediate between *phaios* and *incanus*, but somewhat nearer the former. Intergradation with *affinis* in Washington and Oregon is confused by the great individual variation or possibly ecological subspeciation of the populations of grouse in that area.

The distinctness of this race from *umbelloides* has long been recognized by collectors and field observers in Idaho, who have usually expressed their awareness by referring the birds to the far distant *togata*.

***Bonasa umbellus umbelloides* (Douglas)**

Gray Ruffed Grouse

Tetrao Umbelloides Douglas. (1829:148), Valley of Rocky Mountains, lat. 54° N., and near source of Columbia east of the Coast and Cascade ranges; restricted type locality—Henry House, Alberta (Todd, 1940:394).

Bonasa umbellus canescens Todd [not "*Bonasa canescens* Sparrm." Menzbier, Vog. Russl., 1, 1895, 480 (see Hartert, 1921:1887)] (1940:395); Abitibi River, lat. 50° 53' N., northern Ontario.

Adult (gray phase).—Similar to corresponding phase of *Bonasa umbellus umbellus* but much less brownish, more grayish and darker, being closest in appearance to gray phase of *phaeos* from which it differs in being paler gray (brown areas paler also) above, less heavily barred below; tarsus feathering more extensive. Gray of feathers of nape, back, and rump, and upper tail coverts and tail smoke gray, lightly vermiculated with fuscous to blackish; brown areas of interscapulars cinnamon brown to russet, heavily blotched with black; brown of upper surface of wings dull Saccardo's umber, speckled and washed with grayish; below more heavily banded than in *umbellus*, less so than in *phaeos*, the brown bands averaging slightly darker than in *umbellus*—pale tawny olive, darkening on the sides and flanks to sepia; tarsus feathered for more than half its length.

Adult (brown phase).—Similar to gray phase but tail tawny olive instead of gray and interscapulars and upper surface of wings slightly more extensively brownish; breast and upper abdomen more washed with tawny buff on the average.

Juvenile (brown phase).—Similar to corresponding plumage of *B. u. umbellus*, but less rufescent, more grayish, the general color of upper parts of head, body, and wings buffy brown to grayish olive brown, the rectrices between wood brown and drab; ventral barrings darker—grayish buffy brown.

Juvenile (gray phase).—Like brown phase but gray, the ground color of upper parts of body and wings and tail grayish drab to ashy hair brown; ventral barrings darker—mummy brown, the under parts less washed with buffy.

Downy young.—Not distinguishable from that of *B. u. umbellus*.

Measurements: Adult male.—Wing, 171-195 (182.6); tail, 144-174 (157.7); culmen from base, 24.4-29.4 (26.3); tarsus, 39.0-45.5 (42.5); middle toe without claw, 35.0-40.6 (37.5); unfeathered part of tarsus, 10.9-24.0 (17.7); 43 specimens from Alberta, northern British Columbia, and Montana. *Adult female*.—Wing, 169-180 (174.6); tail, 125-134 (130.4); culmen from base, 23.6-27.6 (25.6); tarsus, 37.5-43.2 (41.0); middle toe without claw, 33.8-36.3 (34.9); unfeathered part of tarsus, 10.9-17.8 (15.3); 11 specimens from Alberta, British Columbia, and Montana.

Distribution.—Subclimax deciduous woodland (aspens, poplar, and willow communities) of the Rocky Mountain Subalpine Forest (Engelmann Spruce-Alpine Fir Association) and the Northern Coniferous Forest (White Spruce-Balsam Fir Association) in the Canadian Life-zone; ranges from northwestern British Columbia (Atlin) southward along the east slopes of the Rocky Mountains to central eastern Idaho and northwestern Wyoming; extends eastward through the aspen parkland and spruce-fir forest of the prairie provinces of Canada, north to middle Manitoba (Oxford House) and south to southwestern Ontario (Lake of the Woods), across Ontario between Lake Superior and James Bay and across Quebec to the north shore of the Gulf of St. Lawrence. (A fine series of specimens from Ontario and Quebec were loaned to us for study by Mr. W. E. C. Todd of the Carnegie Museum, but at Mr. Todd's request the exact localities are omitted here, as they are all to be reported in his work on the birds of the Labrador Peninsula.)

Although specimens from northern Ontario and middle Quebec average slightly darker and have a greater proportion of the tarsus unfeathered than typical *umbelloides* from the east slopes of the Canadian Rockies, the difference seems to be too slight to recognize as a distinct subspecies. These characters merely indicate the trend toward intergradation between *umbelloides* and *togata*. However, the northern Ontario birds are much nearer to *umbelloides* than to *togata*. Therefore *canescens* Todd becomes a synonym of *umbelloides*. Ruffed grouse recorded farther east in Quebec (Anticosti Island, Natashquan and Wolf Bay) and in southeastern Labrador (Hamilton Inlet and Sandwich Bay) may belong to this race also, but no specimens from these regions have been examined in the present study.

Specimens from southern Manitoba (Shoal Lake and Carberry) are intermediate between *umbelloides*, *incanus*, and *medianus*, but on average characters, particularly relatively short unfeathered tarsus, they seem a little closer to *umbelloides*.

***Bonasa umbellus incanus* new subspecies**

Hoary Ruffed Grouse

Type.—No. 155869 United States National Museum (Biol. Surv. Coll.); adult male (brown phase); Barclay, 15 miles east of Salt Lake City, Utah; collected May 1, 1897, by E. A. Preble; original number 253.

Adult (brown phase).—A very ashy bird, similar not to brown but to gray phase of *B. u. umbellus*, but paler and, except for tail, less brownish, more like that of *Bonasa umbellus umbelloides* but paler and less brownish on interscapulars, back, and upper surface of wings; general coloration of forehead, crown, occiput, nape, upper back, and upper wing coverts, light neutral gray, tinged or mixed with from pale light brownish olive to pale tawny olive, the head and nape with very little of this brownish wash; interscapulars with large fuscous to black blotches on feathers, these otherwise ashy tillleul buff, basally washed with pale ochraceous tawny; feathers of lower back, rump, and upper tail coverts snuff brown, tipped, edged, and vermiculated with ashy light neutral gray and with subterminal large tear-shaped tillleul buff to whitish shaft spots, laterally narrowly edged with black and sparingly speckled with the same; rectrices cinnamon buff to pale clay color, the lateral feathers palest, the terminal inch pale smoke gray traversed by broad band of dark dull sepia and sparingly speckled with fuscous, the broad dark band occupying more than half the width of gray area and breaking up into a mass of frecklings on median pair of rectrices; below as in *B. u. umbellus*, but barrings more numerous, especially on abdomen, and averaging paler—pale ashy buffy drab, and the tarsus more fully feathered.

Adult (gray phase).—Similar to brown phase but with tail feathers smoke gray with no buffy tone; ventral barrings dusky—light brownish olive darkening to sepia on the sides and flanks.

Juvenile.—None seen.

Downy young.—None seen.

Measurements: Adult male.—Wing, 172-191 (181); tail, 138-164 (151.8); culmen from base, 25.3-28.8 (27.0); tarsus, 40.3-44.9 (42.6); middle toe without claw, 35.0-39.9 (37.4); unfeathered part of tarsus, 12.0-22.5 (17.4); 20 specimens from Wyoming, Utah, North Dakota, and southeastern Idaho. *Adult female.*—Wing, 165-178 (171.5); tail, 120-147 (133.2); culmen from base, 25.0-27.8 (26.3); tarsus, 36.9-44.7 (39.8); middle toe without claw, 33.2-38.8 (35.0); unfeathered part of tarsus 13.8-21.7 (17.3); 8 specimens from Utah, North Dakota, and northeastern Idaho.

Distribution.—Subclimax deciduous woodland and thickets (cottonwood, aspen, and willow communities) chiefly of the Rocky Mountain Montane Forest (Ponderosa Pine-Douglas Fir Association), Transition Zone, but to some extent also in similar subclimax deciduous communities in the lower fringe of the Rocky Mountain Subalpine Forest (Engelmann Spruce-Alpine Fir Association), Canadian Life-zone; ranges from west-central and central-northern Utah, southeastern Idaho and central western Wyoming, northeastward across Wyoming and the Dakotas to northeastern North Dakota (Walhalla) wherever suitable habitat occurs in this predominantly grassland area. *Bonasa umbellus incanus* intergrades with *umbelloides* in northwestern Wyoming, and southern Manitoba, and probably also in the intervening areas wherever the species occurs in the aspen parklands and along cottonwood bordered streams. This race probably extends to the southern limits of the species' range in the Rocky Mountains and Great Plains region in southwestern and north-central Colorado (Nucla and Estes Park), and in southeastern and central southern South Dakota (Custer State Park and Rosebud). No specimens have been seen to establish this definitely however.

***Bonasa umbellus yukonensis* Grinnell**

Yukon Ruffed Grouse

Bonasa umbellus yukonensis Grinnell (1916:166); Forty-mile, Yukon Territory, on Yukon River, near Alaska boundary.

Adult (gray phase).—Similar to that of *Bonasa umbellus umbellus* but much paler, the palest of all races of the species, the whitish areas above more extensive and purer white, less washed with buffy; nearest to gray phase of *incanus* but paler, with more white and with the most extensive tarsal feathering of all subspecies; gray areas of upper parts of head, body, wings, and tail pale neutral gray to smoke gray, the brown, which is restricted to top of head, interscapulars, wings, and middle of back, is pale tawny olive to pale Saccardo's umber; below as in *B. u. umbellus* but more abundantly barred with buffy drab.

Adult (brown phase).—Similar to gray phase but with tail between sayal brown and Saccardo's umber, distally vermiculated and washed with smoke gray, feathers of interscapular area, back, and rump with very broad transverse subterminal bands of mummy brown (these bands present but concealed in gray phase); ventral barrings darker—Dresden brown to mummy brown.

Juvenile.—Above much grayer than any available juveniles of *B. u. umbellus*; nearest to specimen of *Bonasa umbellus umbelloides*, the general coloration of upper side of head, body, and wings being drab to hair brown, the interscapulars, scapulars, crown, and upper back being broadly and transversely blotched with fuscous to black, with pale tillleul buff shaft streaks and narrow cross bars of slightly darker tillleul buff; rectrices as in *umbelloides* but slightly more washed with drab.

Downy young.—None seen.

Measurements: Adult male.—Wing, 174-190 (182); tail, 129-168 (148.5); culmen from base, 24.9-29.1 (26.8); tarsus, 38.3-45.0 (42.4); middle toe without claw, 34-38.5 (36.7); unfeathered part

of tarsus, 8.8-15.7 (11.2); 34 specimens from Alaska, Mackenzie and northern Alberta. *Adult female*.—Wing, 170-182 (177.6); tail, 127-137 (130.8); culmen from base, 24-27.9 (26.6); tarsus, 38.8-43.5 (41.2); middle toe without claw, 33-37 (34.9); unfeathered part of tarsus, 7.3-14.9 (11.0); 10 specimens from Alaska, Mackenzie, and northern Alberta.

Distribution.—Subclimax deciduous woodlands (willow, aspen, poplar, and birch communities) chiefly in White Spruce-Lodgepole Pine and Black Spruce-American Larch associations, which form the ecotone between the Northern Conifer and Tundra biomes (Hudsonian Life-zone); ranges from western Alaska (Akiak and Nulato) eastward across Alaska, chiefly in valleys of Yukon and Kuskokwim rivers, and across Yukon from Selkirk and the Lewes River Valley, north to La Pierre House, east at least to Great Slave Lake, Mackenzie, and Lake Athabaska, Alberta; extends southward along Liard River, at least to Liard, Mackenzie, and along Athabaska River to Fort McMurry, Alberta. There are records of ruffed grouse from farther east in the Hudsonian Life-zone of northern Manitoba (Brochet and York Factory) which may also belong to this race, but specimens have not been seen to substantiate this. Although primarily a Hudsonian-Zone form, *yukonensis* apparently includes within its range a sizeable area characterized by pure coniferous forest climax (Canadian Life-zone) in southwestern Mackenzie and northern Alberta.

ECOLOGICAL CLASSIFICATION OF BONASA UMBELLUS

Boreal Region

Hudsonian Life-zone

Northern Conifer-Tundra Ecotone (chiefly in subclimax communities)

White Spruce-Lodgepole Pine, and

Black Spruce-American Larch associations

Bonasa umbellus yukonensis

Canadian Life-zone

Spruce-Fir Biome (chiefly in subclimax communities)

White Spruce-Balsam Fir Association (Boreal Forest)

Bonasa umbellus umbelloides

Engelmann Spruce-Alpine Fir Association (Rocky Mt. Subalpine Forest)

Bonasa umbellus umbelloides

Lodgepole Pine-Mountain Hemlock Association (Sierran Subalpine Forest)

Bonasa umbellus affinis

Red Spruce-Fraser Fir Association (Appalachian Subalpine Forest)

Bonasa umbellus monticola

Temperate Region

Transition Life-zone

(1) Northern Conifer-Deciduous Forest Ecotone (in climax and subclimax communities)

Eastern White Pine-Sugar Maple-Eastern Hemlock Association (Lake Forest)

Bonasa umbellus togata

Eastern Hemlock-Yellow Birch Association (Appalachian Montane Forest)

Bonasa umbellus monticola

(2) Grassland-Northern Conifer Ecotone (in climax and subclimax communities)

American Aspen-Paper Birch Association (Aspen Parkland)

Bonasa umbellus umbelloides > *incanus* (intermediate)

(3) Western Mountain Transition Biome (chiefly in subclimax communities)

Ponderosa Pine-Douglas Fir Association (Rocky Mt. Montane Forest)

Bonasa umbellus incanus

Bonasa umbellus umbelloides

Sugar Pine-Ponderosa Pine Association (Sierran Montane Forest)

Bonasa umbellus affinis

Western Larch-Western White Pine Association (Idahoan Montane Forest)

Bonasa umbellus phaios

(4) Pacific Moist Forest Biome (chiefly in subclimax communities)

Western Red Cedar-Western Hemlock Association (Northwest Rain Forest)

Bonasa umbellus sabinii

Bonasa umbellus castaneus

Bonasa umbellus brunnescens

Upper Austral Life-zone

Eastern Deciduous Forest Biome (in climax and subclimax communities)

White Oak-Pitch Pine Association (Atlantic Pine-Oak Forest)

Bonasa umbellus umbellus

Red Oak-Beech-Tulip Association (Mixed Mesophytic Forest)
Bonasa umbellus umbellus
Bonasa umbellus monticola
 White Oak-Shagbark Hickory Association (Oak Grove Savannah)
Bonasa umbellus medianus

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