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16 Ruffed Grouse

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Ruffed Grouse

Bonasa umbellus (Linnaeus) 1776

OTHER VERNACULAR NAMES

*B*IRCH partridge, drummer, drumming grouse, long-tailed grouse, mountain pheasant, partridge, pine hen, pheasant, tippet, white-flesher, willow grouse, wood grouse, woods pheasant.

RANGE

Resident in the forested areas from central Alaska, central Yukon, southern Mackenzie, central Saskatchewan, central Manitoba, northern Ontario, southern Quebec, southern Labrador, New Brunswick, and Nova Scotia south to northern California, northeastern Oregon, central Idaho, central Utah, western Wyoming, western South Dakota, northern North Dakota, Minnesota, central Arkansas, Tennessee, northern Georgia, western South Carolina, western North Carolina, northeastern Virginia, and western Maryland. Recently introduced in Nevada and Newfoundland (modified from *A.O.U. Check-list*).

SUBSPECIES (ex Aldrich and Friedmann, 1943)

B. u. umbellus (Linnaeus): Eastern ruffed grouse. Resident in wooded

areas of two regions, from east central Minnesota, southern Wisconsin, and southwestern Michigan south to central Arkansas, extreme western Tennessee, western Kentucky, and central Indiana (this population sometimes separated as *B. u. mediana* Todd 1940), and from central New York and central Massachusetts south to eastern Pennsylvania, eastern Maryland (formerly), and New Jersey.

B. u. monticola Todd: Appalachian ruffed grouse. Resident from southeastern Michigan, northeastern Ohio, and the western half of Pennsylvania south to northern Georgia, northwestern South Carolina, western North Carolina, western Virginia, and western Maryland.

B. u. sabini (Douglas): Pacific ruffed grouse. Resident of southwestern British Columbia (except Vancouver Island and the adjacent mainland) southwest of the Cascade Range, through west central Washington and Oregon to northwestern California.

B. u. castanea Aldrich and Friedmann: Olympic ruffed grouse. Resident of the Olympic Peninsula and the shores of Puget Sound south to western Oregon.

B. u. brunnescens Conover: Vancouver Island ruffed grouse. Resident of Vancouver Island and adjacent mainland south to Puget Sound and north at least to Lund.

B. u. togata (Linnaeus): Canadian ruffed grouse. Resident from northeastern Minnesota, southern Ontario, southern Quebec, New Brunswick, and Nova Scotia south to northern Wisconsin, central Michigan, southeastern Ontario, central New York, western and northern Massachusetts, and northwestern Connecticut.

B. u. affinis Aldrich and Friedmann: Columbian ruffed grouse. Resident from central Oregon northward, east of the Cascades through the interior of British Columbia to the vicinity of Juneau, Alaska (not recognized in *A.O.U. Check-list*).

B. u. phaia Aldrich and Friedmann: Idaho ruffed grouse. Resident from southeastern British Columbia, eastern Washington, and northern Idaho south to eastern Oregon and on the western slopes of the Rocky Mountains to south central Idaho.

B. u. incana Aldrich and Friedmann: Hoary ruffed grouse. Resident from extreme southeastern Idaho, west central Wyoming, and northeastern North Dakota south to central Utah, northwestern Colorado (rarely), and western South Dakota.

B. u. yukonensis Grinnell: Yukon ruffed grouse. Resident from western Alaska east, chiefly in the valleys of the Yukon and Kuskokwim rivers, across central Yukon to southern Mackenzie, northern Alberta, and northwestern Saskatchewan.

B. u. umbelloides (Douglas): Gray ruffed grouse. Resident from extreme

southeastern Alaska, northern British Columbia, north central Alberta, central Saskatchewan, central Manitoba, northern Ontario, and central Quebec south, east of the range of *affinis* and *phaia*, to western Montana, southeastern Idaho, extreme northwestern Wyoming, southern Saskatchewan, southern Manitoba, southern Ontario, and across south central Quebec to the north shore of the Gulf of St. Lawrence, probably to southeastern Labrador.

MEASUREMENTS

Folded wing: Adult males, 171–93 mm; adult females, 165–90 mm (males of all races average 178 mm or more; females usually average under 178 mm).

Tail: Adult males, 130–81 mm; adult females, 119–59 mm (males average more than 147 mm; females average less than 142 mm).

IDENTIFICATION

Adults, 16–19 inches long. Both sexes have relatively long, slightly rounded tails that are extensively barred above and have a conspicuous subterminal dark band. The neck lacks large areas of bare skin, but both sexes have dark ruffs. Feathering of the legs does not reach the base of the toes; the lower half of the tarsus is essentially nude. Both sexes are definitely crested, but the feathers are not distinctively colored. In addition males have a small comb above the eyes that is orange red and most evident in spring. Most races (*castanea* is perhaps the only exception) exist in both gray and brown phases, which appear with the first-winter plumage. Otherwise, little seasonal, sexual, or age variation occurs. The birds are generally wood brown above, with blackish ruffs (less conspicuous in females and immatures) on the sides of the neck, and with small eye-spot markings on the lower back and rump (less conspicuous in females). The tails of both sexes have seven to nine alternating narrow bands of black, brown, and buff, followed by a wider subterminal blackish band that is bordered on both sides with gray and is less perfect centrally in females and some (presumably first-year) males. In winter, both sexes develop horny pectinations on the sides of their toes, which are more conspicuous than in most other species.

FIELD MARKS

The fan-shaped and distinctively banded tail and neck ruffs of both sexes make field identification easy. The birds usually take off with a

conspicuous whirring of wings, and in spring males are much more often heard drumming than they are seen.

AGE AND SEX CRITERIA

Females have shorter tails than do males (see above) and their central tail feathers lack complete subterminal bands near the middle of the tail. A mottled pattern on the central tail feathers (which occurs in about 15 percent of the population) can indicate either sex, but a bird with this characteristic is twice as likely to be a male as a female (Hale, Wendt, and Halazon, 1954). Females also have little or no color on the bare skin over the eye, whereas in males this area is orange to reddish orange (Haber, in Mosby, 1963). Davis (1969a) reported that the length of the plucked and dried central rectrices provides a 99 percent effective means of determining sex of both adult and immature ruffed grouse, but specific separation points for these groups vary with populations.

Immatures can be identified by the pointed condition of their two outer primaries, especially the outermost one. Davis (1969a) stated that during the hunting season the condition of the tenth primary was useful for determining age of nearly 60 percent of the birds, with only a 2 percent error. However, the presence of sheathing at the base of the outer two primaries (adults) or on the eighth but not the ninth or tenth primaries (immatures) separated 79 percent of the birds examined with a 3 percent error. Immature males can be distinguished from adults by their shorter central tail feathers (length of plucked feather, 159 mm or less, compared to at least 170 mm in adults) as well as various other criteria (Dorney and Holzer, 1957). Ridgway and Friedmann (1946) report that the two outer primaries of immatures have outer webs that are pale fuscous and mottled or stippled with lighter buff, instead of being buff or whitish with darker brown markings.

Juveniles resemble the adult female but have barred tail feathers that lack the heavy subterminal band and have the gray tips poorly developed (Ridgway and Friedmann, 1946). Juveniles also have white rather than buff chins and primaries with more mottling on their outer webs (Dwight, 1900).

Downy young are illustrated in color plate 61. Downy ruffed grouse can readily be identified by the restriction of black on the head to an elongated ear-patch that is narrowly connected to the eyes and a few midcrown spots. The crown is otherwise a uniform ochraceous tawny, gradually blending with the buffy face color. The back lacks definite patternings and varies from russet or dark brown dorsally to pale buff or yellow ventrally.

DISTRIBUTION AND HABITAT

The distribution of the ruffed grouse in North America covers a surprising variety of climax forest community types, from temperate coniferous rain forest to relatively arid deciduous forest types. The unifying criterion, however, is that successional or climax stages include deciduous trees, especially of the genera *Betula* and *Populus*. For example, the range of the balsam poplar (*Populus balsamifera*) bears a surprising similarity to that of the ruffed grouse, as does that of the paper birch (*Betula papyrifera*). Aldrich (1963) correlated racial variation in the ruffed grouse with major plant formations. He indicated that *togata* occurs in northern hardwood-conifer ecotone area, *umbellus* and *monticola* in eastern deciduous forest, *mediana* in oak-savanna woodland, *umbelloides* in typical boreal forest, *yukonensis* in northern or "open" boreal areas, *incana* in drier montane woodlands and aspen parklands, *brunnescens*, *castanea*, and *sabini* in the Pacific coast rain forest, and *phaia* in the corresponding wet interior forest. The relatively drier montane woodlands of the Pacific northwest are occupied by *affinis*. Not only is there a correlation between the relative wetness or dryness of these general habitat types and associated darkness or paleness of the body plumage, but there are also some relationships between climate or vegetation and color phases. The gray phase of ruffed grouse is typically associated with northern areas or higher altitudes, while the reddish brown color phase is more characteristic of southern and lower altitude populations. Gullion and Marshall (1968) have discussed the ecological significance of color phases in ruffed grouse, and they suggest that gray-phase birds are perhaps physiologically better adapted to cold than are red-phase ones, and predominate in conifers and aspen-birch forest of these colder areas. They also suggest that gray-phase birds may be less conspicuous in boreal forests, while in the hardwood forests where raptors have poorer hunting conditions and mammalian predators are more important the color phase may not be significant. However, their data indicate that gray-phase birds survive relatively better in hardwood than do red-phase ones, and both phases survive better in hardwoods than in conifers.

Gullion (1969) has pointed out that on a continent-wide basis, the areas of highest population density of ruffed grouse correspond to the distributional patterns of aspens (*Populus* spp.), which he related to winter as well as summer food use by adults, as well as their value as brooding habitat. Weeden (1965b) reported that ruffed grouse habitat in Alaska typically contains large amounts of aspen and usually also contains white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). Where ruffed and spruce grouse

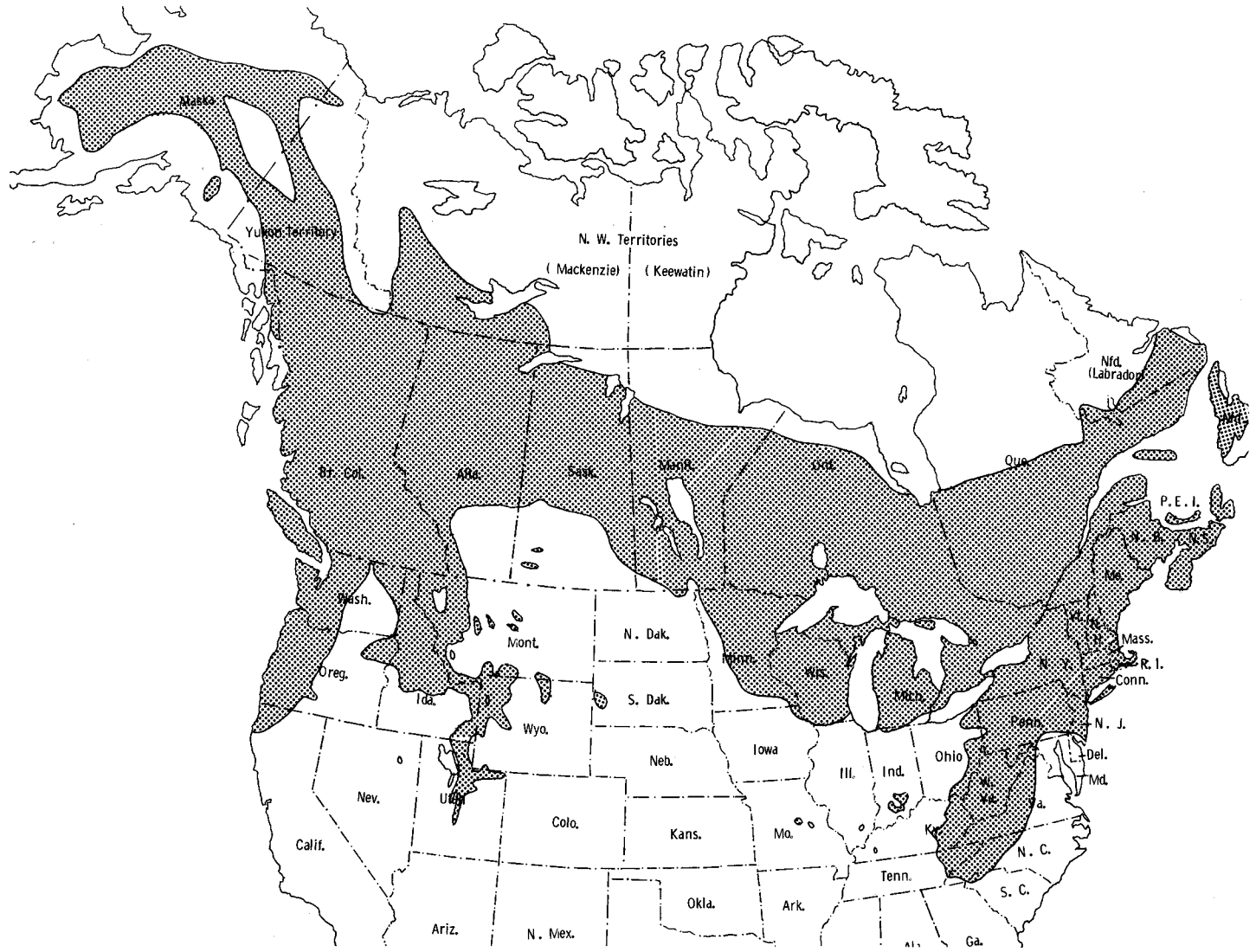


FIGURE 29. Current distribution of the ruffed grouse.

occur together in Alaska, the ruffed are found in earlier stages of succession, frequenting edges, shrubby ravines, and similar openings. Likewise in southern Ontario I have noticed that both species may be found within a hundred yards or less of one another, but ruffed grouse are always associated with birch or poplar, while spruce grouse are usually to be found under coniferous cover such as jack pine.

Edminster (1947) has analyzed the general shelter requirements of the ruffed grouse in the northeastern states according to vegetational succession stages. Open land types dominated by herbaceous plants provide some food sources for grouse but are of secondary importance. Overgrown fields with shrubs and saplings include single-species stands of high quality quaking aspen cover (*Populus tremuloides*), pin cherry (*Prunus*), scrub oak (*Quercus*), or alder (*Alnus*) cover of moderate quality, and low quality gray birch or hardhack cover. Other important cover types include mixed-species stands of hardwood shrubs and trees and mixtures of hardwood and coniferous species. Slashings following lumbering activities produce an early stage dominated by many shrubs and herbaceous species, especially blackberries and raspberries (*Rubus* spp.), of considerable value to grouse. A later, thicker stand of saplings and taller trees is of less value, especially for young birds.

Older forest stands in the northeast include hardwood types, mixed hardwoods and conifers, and predominantly coniferous forest types. Edminster reported that younger hardwood stands have better undercovers for grouse than older stands and that scattered openings improve the value of either age class. Pasturing also may affect the undercover development. Edminster believes that hardwoods with about 20 percent coniferous species provides better cover than pure hardwood stands and that those woodlands with from 20 to 70 percent conifers provide both food and cover at all seasons, although summer cover may be imperfect. Predominantly coniferous stands of trees may be food-deficient in younger stages, but in mature stands with a hardwood understory this is not the case.

A study by Dorney (1959) in Wisconsin provides some additional information on grouse-forest relationships. Dorney also reported that mixtures of hardwoods and conifers have greater ruffed grouse use than do hardwoods alone, but Wisconsin grouse appear to be less dependent on conifers for cover than is the case in New York. A heavy shrub understory is needed by grouse for drumming sites, and an absence of shrubs in young hardwood stands causes rapid loss of drumming territories.

Gullion (1969) reported that in Minnesota young aspen stands first become habitable by adult ruffed grouse about four to twelve years after regeneration following logging or fire, when the trees are twenty-five to thirty feet tall and the stem densities are less than six thousand per acre.

Grouse continue to use the habitat throughout the year for the next ten to fifteen years, until stem densities drop below about two thousand per acre. Older stands of aspen provide important winter food in the form of male flower buds besides providing nesting habitats.

The importance of small clearings in deciduous forest, as found by Edminster, was proved by Sharp (1963), who established a number of small clearings $\frac{1}{4}$ to 1 acre in size in half of a 1,470-acre pole timber forest. These changes were initiated in 1950, and during the next five years from seven to twenty-one broods used the managed area, while two to three used the unmanaged portion of the forest. After ten years, the openings in the forest had filled in, and the value of the area for brood use had declined.

Probably the over-all range of the ruffed grouse has not changed greatly in historical times. Slight additions to the range have occurred with introductions. Wild-trapped grouse from Nova Scotia, Wisconsin, and Maine have apparently been successfully introduced into Newfoundland (Tuck, 1968), and they have also been successfully introduced in the Ruby mountain range of northeastern Nevada (McColm, 1970).

Restrictions in ranges have occurred in a number of states, as indicated by Aldrich (1963). Although it once occurred in northeastern Nebraska, the ruffed grouse is now completely extirpated from the state. It is also gone from northeastern Kansas and northeastern Alabama (*A.O.U. Check-list*, 1957). However, a specimen was recently collected in Jackson County, Alabama (*Audubon Field Notes*, 21:15, 1967). The population in Missouri was probably never high and may have declined to less than one hundred birds by the 1930s, although recent attempts at reintroduction have had some success (Lewis, McGowan, and Baskett, 1968). By 1930 the once extensive Iowa population was also nearly gone except for a remnant in northeastern Iowa. This population still persists in good numbers locally, and hunting for the first time in 45 years was allowed in 1968 (Klonglan and Hlavka, 1969). In Ohio, where grouse once ranged over the entire state, a low ebb was reached about 1900, and the species was protected for thirty-two of thirty-four years following 1902 (Davis, 1969b). Remnant populations occur in southern Illinois, where the species is protected. The species is also protected where it occurs in northwestern South Carolina, which is at the extreme southern limit of the species' range. Although limited to a small area of southern Indiana, the grouse population there has been fairly stable for the last two decades and is distributed through about eleven hundred square miles in five counties. In 1965 the first limited season was held since 1937.

POPULATION DENSITY

Grouse populations have been intensively studied in New York by Bump

et al. (1947), who reported breeding densities of from eight to twenty-two acres per bird near Ithaca and from twenty-one to thirty-eight acres per bird in the Adirondacks. Maximum fall densities in the two areas ranged from five to twenty acres in various years. Gullion (1969) estimated that maximum breeding densities in Minnesota allowed by territorial behavior are one pair (i.e., 1 territorial male) per eight to ten acres, although normal area-wide densities are more commonly 4 to 6 birds per one hundred acres. Slightly lower breeding densities of 2 to 4 birds per one hundred acres occur in Ohio (Davis, 1968). Porath (cited in Klonglan and Hlavka, 1969) estimated a spring breeding density of 30 to 35 birds per square mile (4.5 to 5.3 birds per one hundred acres) in northeastern Iowa, while late summer populations were approximately 90 to 135 birds per square mile in the same area. In Indiana, Thurman (1966) reported a spring density of 18 males per square mile.

Consideration of ruffed grouse densities are not complete without mention of the well-known cycles of population abundance that have been reported for several grouse species but are especially often attributed to the ruffed grouse. Keith (1963) has made an intensive survey of population fluctuations in a variety of birds and mammals in northern North America, and his conclusions appear to be well founded. He believed that the ruffed grouse has undergone fairly synchronous ten-year population cycles at local, regional, and continental levels over most of its North American range with the exception of the eastern United States and New Brunswick. His book summarizes population density figures from a variety of studies in Minnesota, Michigan, and Wisconsin that indicate peak-year fall densities of from 123 to 180 birds per square mile in Michigan and up to 353 birds per square mile in Minnesota. The average ratios between densities of peak years and those of the subsequent low ones range from a ratio of 3:1 to as much as 15:1, with twelve such estimates averaging about 8:1.

In seven studies of local grouse populations, the ruffed grouse had peak populations or initial declines the same year as prairie grouse and spruce grouse, in two cases the ruffed grouse peaked or declined a year before the others, and in four cases the other grouse peaked or began declines one to three years before the ruffed. Likewise, at state or provincial population levels, the ruffed grouse peaked or began declines the same year as the prairie grouse in six of fourteen cases, while in six cases the other grouse peaked or declined one to three years before the ruffed grouse, and in the remaining two cases the ruffed grouse peaked or began its decline a year before the others (Keith, 1963).

HABITAT REQUIREMENTS

Wintering Requirements

Although the ruffed grouse is one of the most temperate-adapted of all North American grouse, as indicated by its distribution in the southeastern states, it is well adapted to withstand cold weather. Edminster (1947) indicates that cold weather alone, if not accompanied by snow or sleet, does not materially affect grouse survival. However, during stormy weather, the grouse resort to coniferous trees or to roosting beneath the snow, where they may remain several days. Although the birds are rarely if ever frozen into such snow roosts, they become highly vulnerable to predation by mammals such as foxes, and Edminster reported mortality rates from 25 to 100 percent higher than normal during a year of unusually heavy snow-roosting activity.

Although conifers provide valuable winter roosting cover for ruffed grouse in New York, the birds continue to rely on hardwood trees for their food, particularly buds and twigs of such trees as poplars, apples (*Malus*), birches, oaks, and cherries (*Prunus*). When available, understory shrubs and vines such as grapes (*Vitis*), greenbrier (*Smilax*), laurel (*Kalmia*), blueberry (*Vaccinium*), and wintergreen (*Gaultheria*) also provide important sources of winter food and cover (Edminster, 1947).

Spring Habitat Requirements

The spring habitat needs of ruffed grouse appear to be closely tied to ecological situations associated with suitable drumming sites, or "activity centers" (Gullion and Marshall, 1968). Within a general activity center, a specific display site, or "drumming stage" must be present, and Gullion and Marshall believe that two factors govern the choice of such a site. These are the presence of a number of forty-to-fifty-year-old aspens near or within sight of a drumming log and also a tradition of occupancy of the site by male grouse. They concluded that the presence of aspens is the most important aspect of cover which regulates the choice of activity centers, and they found strong relationships between cover types and male survival. Males survived best in hardwoods completely lacking evergreen conifers (which is in contrast to conclusions mentioned earlier by Edminster), but the presence of spruce and balsam fir (*Abies balsamea*) did not reduce survival. However, survival did decrease as the density of mature pines increased, and male grouse did not survive as well in edge situations as in uniform forest types.

Boag and Sumanik (1969) gathered evidence supporting the view that ruffed grouse do not select drumming sites at random, but that the nature of the surrounding vegetation plays an important role. Comparing eighty drumming sites with ninety-eight similar sites that were not used, they found shrub sizes greater at used than unused sites, and canopy coverage as well as the frequency of young white spruce trees was higher at used sites. Only at used sites was aspen the predominant tree species in the tree layer. They believe that selective pressure for the male to choose open and visually effective sites for drumming is counterbalanced by selection favoring sites protected from predators. The result has been selection favoring sites which give the males sufficient height above the ground from which to observe other grouse or large ground predators, sufficient openings in the shrub layer to see at least twenty yards in most directions, and sufficient canopy and stem coverage to screen the birds from aerial predators. These conditions are met in Alberta by those areas where the density of young hardwood trees and the density and canopy coverage of young spruce are the highest.

The specific drumming stage is usually but not always a log, thus the presence of logs in suitable habitats is an important component of spring ruffed grouse habitat. Palmer (1963) analyzed forty drumming logs in Michigan that had been regularly used by male grouse. Of the total, thirty-four were old, decayed conifers, primarily pines. Males always drummed near the larger end of these, usually about 5 feet from the end. The logs ranged from seven to twenty-one inches in height at the drumming position, and none was shorter than 5.5 feet long. Vegetation over 8 feet high was significantly more dense near the logs than in the surrounding cover, and among the larger shrubs, speckled alder (*Alnus incana*) comprised about three-fourths of the sampled stems. In general, drumming sites were associated with ground vegetation less dense, and large shrub and tree cover more dense, than was typical of the surrounding general vegetation.

Several studies have indicated that a male grouse may utilize more than one log in his territory for drumming purposes, but one is typically favored. Gullion (1967a) called this log the "primary log," and designated additional drumming sites as "alternate logs." Disturbance may force the bird to use yet other "secondary logs." Logs and activity sites may also be classified as perennial if they are used through the lifetimes of a succession of grouse, or transient if they are used by one grouse and not used again for several years by other birds. Although perennial logs apparently supply the appropriate ecological conditions that attract male grouse, Gullion and Marshall (1968) have found that male grouse using such sites suffer higher mortality as an apparent result of predators' learning the locations of favored display areas.

Nesting and Brooding Requirements

Habitats selected by female grouse for nesting have been analyzed by Edminster (1947), based on the study of 1,270 nests in New York. Medium-aged stands of hardwoods, with a few conifers, was most commonly used for nesting habitat, followed by medium-aged stands of mixed hardwoods and conifers. When consideration is given to relative cover availability, slashings were also found to be of importance as grouse nesting habitat in New York. Middle-aged stands of hardwoods or mixed stands were found to be considerably more valuable as nesting habitat than were mature forest habitats. As to specific nest sites, the bases of trees appeared to be the most favorable site, being used about two-thirds of the time. Most of these trees were hardwoods, and nearly all were of considerable size. Most of the remaining nest sites were at the bases of tree stumps, under logs, bushes, or brush piles. Edminster concluded that nest sites are chosen to provide a combination of visibility, protection, an escape route, and proximity to edges and to satisfy an apparent desire for sunlight. The undergrowth nearby is usually open and the canopy density is also relatively open. More than half of the nests were within fifty feet of a forest opening, often the edge of a road. Slope considerations are evidently not important, except that steep slopes are avoided.

Gullion (1967b, 1969), summarizing research done at Cloquet, Minnesota, reported that female grouse probably begin a search for a clone of male aspen trees after mating, near which they locate their nests. These trees are then used by the incubating hens for foraging during incubation.

Brood habitat analyses have also been made by Edminster (1947). Based on studies of 1,515 broods in New York, it was clear that females with broods showed a preference for brushy habitats, especially overgrown land, followed by slashings. Hardwood stands that have been "spot-lumbered" exhibited a high brood usage, as has been later confirmed by studies in Pennsylvania by Sharp (1963). At the same time, hardwood forests continue to receive heavy use from adult grouse (males and broodless females) during the summer, while mixed woods and coniferous forest types serve for escape from extreme heat and summer storms.

FOOD AND FORAGING BEHAVIOR

Korschgen (1966) has analyzed the nutritional value of seasonal foods of ruffed grouse in Missouri and concluded that high-protein foods are taken in greatest amounts during summer, foods high in fat and carbohydrate were taken most during winter, and the largest amounts of mineral sources were

taken during times of reproduction. Evidently grouse select food to fulfill seasonal nutritional needs. Korschgen summarized the principal ruffed grouse foods indicated by twenty-four published studies. Aspen and poplars are listed as principal foods in seventeen of these studies, birch in eleven, and all other food sources were mentioned less often, with apple, grape, sumac, beech, and alder all being listed in several studies. In analyses of foods from six areas in the eastern United States, Martin, Zim, and Nelson (1951) list aspen as being of first or second importance in five areas, and lacking only in samples from the Virginia Alleghenies. Other plants listed in several studies are clover, greenbrier, hazelnut, and grape.

Winter foods of the ruffed grouse consist largely of buds and twigs of trees. Edminster (1954) lists the following major winter sources of such foods: birches (several species), apple, hop hornbeam (*Ostrya*), poplar, cherry, and blueberry. In the Cloquet area of Minnesota, aspens (*Populus tremuloides* and *P. grandidentata*) are usually the most important source of winter foods, and with the appearance of the male catkins in late winter these trees provide the most nutritious food source available to ruffed grouse as long as snow is on the ground (Gullion, 1969).

A study in Utah by Phillips (1967) indicated that chokecherry (*Prunus virginiana*) was the most preferred winter food, followed closely by aspen and maple (*Acer*). Aspen was also the second most important fall food, but hips from roses (*Rosa*) had higher usage. In Ohio, Gilfillan and Bezdek (1944) found that the fruit and leaves of greenbrier (*Smilax*) had high winter use, as well as aspen buds, fruit of dogwood (*Cornus*), grape (*Vitis*), sumac (*Rhus*), beech (*Fagus*), and other plants. Winter food in Maine, as reported by Brown (1946), consisted primarily of buds of aspens, followed by buds and leaves of willows, catkins and buds of hazelnut (*Corylus*), and the buds of wild cherry and apple.

Following winter, as ground vegetation is exposed, food consumption of ruffed grouse becomes more diversified, but at least in New York the buds of poplar, birch, cherry, hop hornbeam, and blueberry are still consumed well into May (Edminster, 1947). Likewise in Maine the buds and catkins of poplar are a primary spring food, in addition to buds and catkins of birch, willow buds, and the leaves of strawberry (*Fragaria*) and wintergreen (*Gaultheria*). In Minnesota, male grouse sometimes continue to feed almost entirely on the male catkins of aspens long after snow melt allows succulent evergreen herbaceous plants to become available (Gullion, 1969). Quaking aspen in this region is preferred over big-toothed aspen by a ratio of more than 2 to 1.

The diet of adult grouse changes drastically in early summer as berries and fruits become available (Edminster, 1947). These fruits include straw-

berries, raspberries and related species of the genus *Rubus*, cherries, blueberries, and Juneberries (*Amelanchier*). Insects comprise a small percentage of adult foods at this time, rarely if ever exceeding 10 percent.

In contrast, the basic food of ruffed grouse chicks for at least the first week or ten days of life consists of insects. Bump et al. (1947) reported that 70 percent of the food taken in the first two weeks consists of insects, compared to 30 percent during the third and fourth week, and dropping to 5 percent by the end of July. Ants are among the most frequent food items, but a variety of other insect types, including sawflies, ichneumon flies, beetles, spiders, grasshoppers, and various caterpillar species make up the remainder of chick foods from animal sources. As dependence on insects declines with age, the amount of plant foods, particularly hedge achenes and the fruits of strawberries, raspberries, blackberries, and cherries increases correspondingly (Bump et al., 1947).

Fall foods for juvenile and adult birds include a variety of fruiting shrubs, such as viburnums, dogwoods, thorn apples, grapes, greenbriers, sumacs, and roses (Edminster, 1954). The availability of many of these persists into winter, when they supplement the standard diet of buds, twigs, and catkins.

Gullion (1966) has emphasized that the abundance of data on fall food intake by gamebirds, is often misleading in that the diversity of foraging indicated during that time of year is not representative of the critical dietary sources needed for the population's survival through the winter. Thus, the availability of a winter source of male catkins of birch, alder, hazel, and particularly aspen is probably the most important single factor influencing the wintering abilities of ruffed grouse. Gullion believed that quantitative or qualitative difference in these winter foods might account for major population fluctuations in Minnesota ruffed grouse. Lauckhart (1957) had earlier pointed out that periodic heavy seed crops in trees may sap the nutrients from buds and stems for a several-year period between such crops, causing a nutrient deficiency for animals highly dependent on these trees. The usual cycle of aspen seed crops is four to five years; thus an interaction of this cycle and some other factor or factors might account for the ten year grouse "cycle." Clearly this idea has great promise and should be investigated thoroughly before being discarded.

The importance of water, either in the form of standing water, dew, or succulent plants, also should not be overlooked for ruffed grouse. Bump et al. indicate that captive grouse can easily survive for at least twelve days without food if they are provided with water but in the absence of both food and water will live only a few days. Since most grouse foods contain considerable water, it is probable that the birds can normally survive indefinitely in the absence of standing water.

MOBILITY AND MOVEMENTS

Ruffed grouse do not perform any movements that might be considered migratory, although there are some seasonal variations in mobility. Little movement is normally exhibited by ruffed grouse broods prior to the brood's breaking up and dispersing; Chambers and Sharp (1958) reported that the cruising radius of most marked broods was no more than a quarter mile. With the dispersal of the broods, more than half of the juveniles moved distances of more than a mile, in one case up to 7.5 miles. Similarly, Hale and Dorney (1963) reported that about one-fourth of the juveniles they banded had moved more than 1 mile from the banding site at the time of recovery. One grouse they banded as a three-month-old juvenile was shot thirty-one days later some 12 miles from the banding site. Apparently these fall movements were independent of population densities and were unrelated to so-called "crazy flight" behavior, during which young grouse may make long and erratic movements apparently related to inexperience and perhaps fright.

By winter, movements of both young and adult grouse decline, and the birds become virtually sedentary by spring. Hale and Dorney (1963) found that males banded on drumming sites were highly sedentary and normally returned to the same site each year. Chambers and Sharp (1958) likewise reported that grouse become sedentary as they mature, with males only rarely moving more than one-fourth mile, while females sometimes moved more than a mile. Hale and Dorney likewise reported that, except during winter, females were consistently more mobile than males. Gullion and Marshall (1968) noted a high degree of fidelity by adult male ruffed grouse not only to a particular territory but also to a specific display site. Only about 36 percent of 168 males that lived at least twelve months or longer moved to another log during their drumming lifetimes, and such movements averaged only about three hundred feet. At least 20 males, however, moved to new activity centers.

Movements by female ruffed grouse during the spring season are of equal interest and have been studied by Brander (1967). By studying the daily movements of three females in early May, Brander found that the females moved from their established winter home ranges of seven to twenty-six acres towards male drumming sites, apparently stimulated by the drumming behavior, particularly drumming sounds. One female was apparently attracted to three different males on different days before copulation occurred, and the pair remained together no more than a few hours. Since the male continued to drum after her departure, Brander concluded that the ruffed grouse mating pattern should be regarded as a promiscuous one. He estimated that the three females each remained in a state of receptivity for

only four days, ending the day before the first egg was laid. The hen located her nest in each case within the area of her movements of the previous week to ten days. As mentioned previously, the female usually seeks out a clone of male aspen near which she establishes her nest (Gullion, 1969).

REPRODUCTIVE BEHAVIOR

Territorial Establishment and Advertisement

According to Bump et al. (1947), captive male grouse begin to exhibit aggressiveness as early as the first of March, although they have sometimes been seen strutting on warm days in winter. Edminster (1947) reported that drumming has been heard every month of the year and every hour of the day and night, but the most intensive drumming in New York occurs in early spring during late March and April, tapering off in May.

The two basic aspects of male reproductive display are drumming ("wing-beating" of Hjorth, 1970) and strutting ("upright," "bowing," and "rush" sequence of Hjorth, 1970). There is no doubt that drumming is primarily an acoustic display and serves to advertise the location of the male in fairly dense forest cover. Strutting, however, is a predominantly visual display, and is probably not normally released except in the visual presence of another grouse or similar stimulus. Undoubtedly both displays are essentially agonistic or aggressive in origin, serving for territorial proclamation and establishment of dominance. Since drumming is the basic means of territorial advertisement, it will be discussed first.

The motor patterns of the drumming display (Figure 30) are well described in Bent (1932) and many other references and need little amplification here. The male typically stands on a small log, facing the same direction and at virtually the same location on each occasion. With his tail braced against the log and his claws firmly in the wood, he begins a series of strong wing-strokes. These strokes, which start slowly at about one second intervals, rapidly speed up, with a complete series lasting about eight (Allen, in Bent, 1932) to eleven seconds (Hjorth, 1970). Hjorth found that in a sample of drumming displays from Alberta there were consistently forty-seven wing-strokes, while one from Ohio has 51. Aubin (1970) noted that among six ruffed grouse studied in southwestern Alberta the number of wing-strokes varied only from forty-four to forty-nine in his samples and was even more consistent for individual birds.

Allen hypothesized that the muffled drumming sound produced by the wings resulted from the forward and upward thrust rather than the return stroke. This strong forward thrust produces a counter pressure that forces

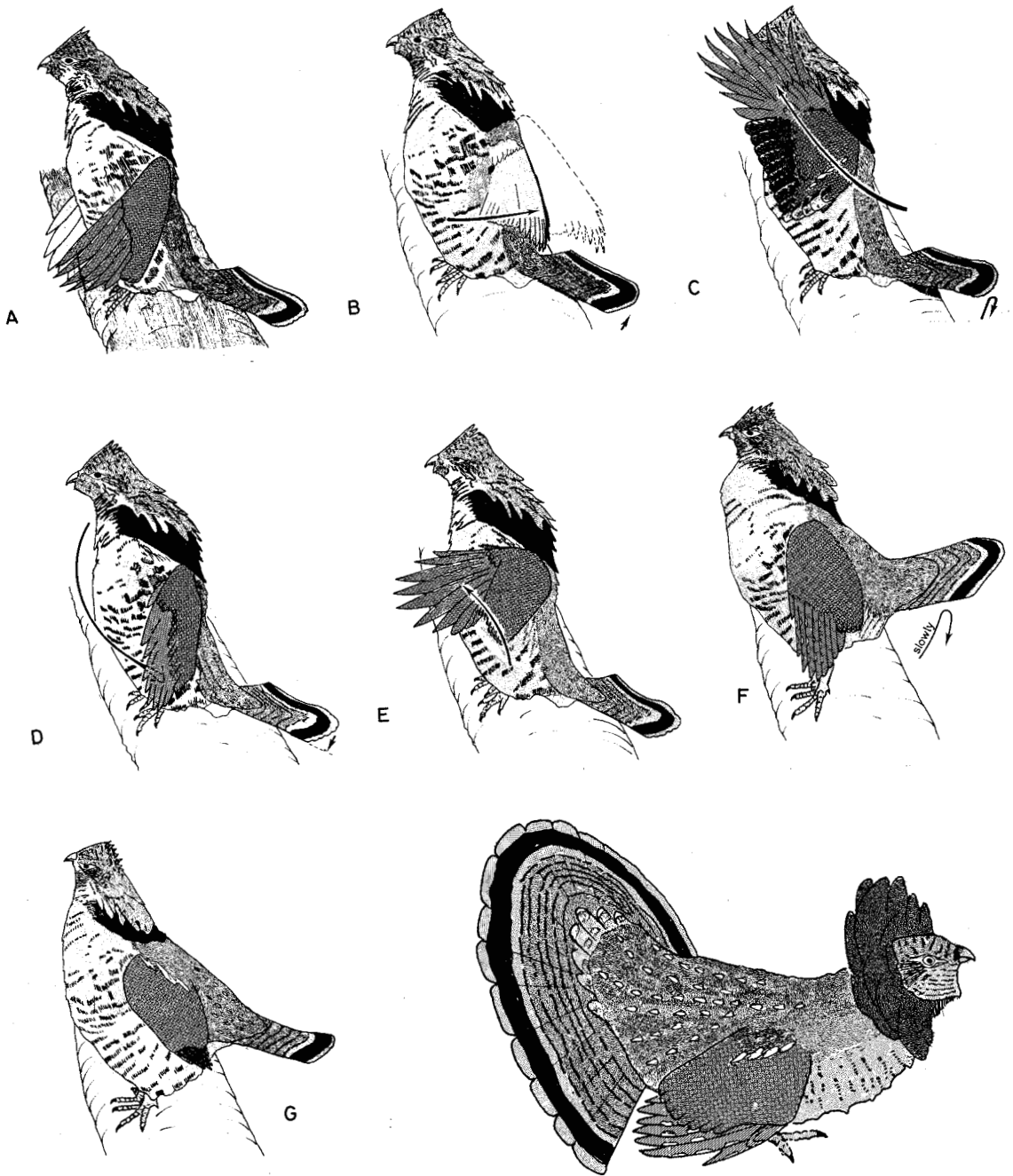


FIGURE 30. Sequence of the drumming display (A-G), and the final stage of the rush display of the ruffed grouse (from Hjorth, 1970).

the bird backward, thus explaining the need for the brace provided by the tail and the importance of clutching the log with the claws. At the end of the last stroke this pressure is released, and the bird tips forward on its perch. As Allen noted, the wings do not touch each other during the drumming, and the noise simply results from air compression, which accounts for the dull throbbing nature of the sound. Recently, Hjorth (1970) has advanced the idea that the downstroke rather than the upstroke may be responsible for this sound.

Drumming usually begins well before daylight and may continue until somewhat after sunrise. It usually begins again about an hour before twilight and may continue until dark (Bump et al., 1947). The usual interval between drumming displays is three to five minutes, but this interval varies from a few seconds to much longer periods.

As noted earlier, most males use a single log on which to drum, but some may use more than one. Bump et al. (1947) reported an average of 1.33 logs per male used by 1,173 grouse, Aubin (1970) found that from 1.5 to 1.7 logs per male were used in different years and independently of population densities, while as noted earlier Gullion and Marshall (1968) noted a certain amount of movement in display sites of male grouse.

Gullion (1967a) found that only a few male grouse establish drumming logs their first fall, and a few also fail to become established the following spring. Most birds occupying logs in his study area were full adults, at least twenty-two months old. He also found a hierarchy of dominance among males. An established male on a drumming log is a "dominant drummer," and within his activity center a second, or "alternate" drummer may occur and take over the site of the dominant drummer if it is killed. Nearby rivals on adjacent activity centers are called "satellite drummers," but these are fairly rare. However, other males are "nondrummers," and drum infrequently or not at all. These are presumably young grouse that have been unable to establish drumming sites.

Gullion (1967a) also found "activity clusters" of males, consisting of from about four to eight males occupying sites in fairly close proximity. These seem to represent an expanded collective display ground, similar to those that have been described for blue grouse.

Gullion reported that males remain closely associated with their display sites during the summer and that fall drumming may approach or even exceed spring drumming activity. At least a few young males, no older than seventeen to twenty weeks, may become established at this time.

Male Strutting Behavior

Presumably the normal releaser for strutting rather than drumming is

the appearance of another grouse near the display log. Edminster (1947) indicates that the drumming male will then strut very slowly toward the intruder, with tail erect and spread. The ruffs on the side of the neck are raised ("upright cum ruff display" of Hjorth, 1970), and the male begins to emit hissing sounds that parallel the tempo of the drumming display. With each hiss the head is lowered and shaken in a rotary fashion ("bowing cum head-twisting and panted hissing" of Hjorth, 1970), giving the impression of a locomotive getting underway (Bump et al., 1947). The display ends with a blur of head-shaking and hissing, followed by a short, quick run toward the other bird as both wings are dragged along the ground ("rush cum prolonged hiss" of Hjorth, 1970). Photographs of this display suggest that in the early stages it is oriented laterally, with the tail and upper part of the body tilted toward the object of the display and the head turned in the same direction. However, the short rush is in a shallow arc toward the other bird (Hjorth, 1970). The similarities of this display to the short rushes of the blue grouse and the spruce grouse are clearly evident. Unlike the spruce grouse, however, the tail is neither shaken nor fanned to produce sound.

Bump et al. (1947) described a "gentle phase" following the strutting phase, which in turn was followed by a "fighting phase" of males. However, their data do not support such a strict interpretation of male behavior patterns nor would such a sequence seem biologically probable. The strutting behavior of males serves equally well as a preliminary threat display toward other males prior to fighting and as a preliminary to attempted copulation with females. The means by which males recognize the sex of intruders on their territories is still uncertain, but in all likelihood there is a differential sexual response of males and females to strutting in another bird. Hjorth (1970) gave the posture associated with this reputed "gentle phase" the name "slender upright cum head-shaking."

The period of receptivity of females is apparently only from three to seven days (Bump et al., 1947; Brander, 1967) and probably is terminated as soon as a successful copulation is achieved. Assumption of the typical receptive posture of grouse, with the wings drooped and slightly spread and the tail slightly raised, while the body feathers are depressed, will stimulate copulation attempts by the male.

Vocal Signals

Hissing is performed by both sexes. Males hiss during their head-shaking and short-rush displays, and females hiss when defending a brood (Bump et al., 1947). Females also utter a squeal during distraction display and quiet their hiding chicks with a downward-inflected scolding note. After any

danger is past, they call the brood together with a low, humming call (Bump et al., 1947). Adult grouse of both sexes utter a startled *pete-pete-pete* note, and a chirping *perrck* note which Bump et al. attributed to "curiosity." A variety of "conversational" notes are also present.

Chicks have four principal call-notes, according to Bump et al. (1947). These include alarm calls, two different notes uttered by scattered chicks, and a warning signal of several descending notes that is uttered by older chicks.

Nesting and Brooding Behavior

Typical nest sites for the ruffed grouse have already been mentioned earlier in the discussion of nesting requirements. Bump et al. (1947) report that the female lays her eggs at an average rate of two eggs every three days, thus taking seventeen days to complete an average clutch of eleven eggs. The attachment of the female to the nest increases as the clutch size increases, but incubation does not begin until the last egg is laid. The period of incubation is from twenty-three to twenty-four days, but low environmental temperatures may delay hatching a few days beyond this time. Bump et al. report that during incubation the female will leave the nest for from twenty to forty minutes, or only rarely longer, to feed. Evidently feeding may occur twice each day under normal conditions, but during stormy weather the bird may remain on the nest continuously. Much enlarged "clocker" droppings are typical of incubating females; these are usually found in the vicinity of nests near the usual foraging areas.

Bump et al. (1947) report that although the average clutch size for 1,473 first nests was 11.5 eggs, 149 renesting attempts averaged only 7.5 eggs. Since no cases of second renesting attempts were found, they estimated that the maximum number of eggs that a female might lay in a single season is about 19. There is no evidence that second broods are ever raised by this or any other species of grouse in North America.

Female ruffed grouse exhibit strong nest and brood defense tendencies and will often resort to a disablement display, feigning a broken wing, especially prior to hatching time. Following hatching, the female more often stands her ground, spreads her tail, and assumes a posture similar to the male's strutting posture as she hisses or utters squealing sounds. When the chicks gain the power of flight after ten or twelve days, the usual response of both hen and chick is to fly when disturbed. By mid-September, when the chicks are twelve or more weeks old, the families begin to break up and dispersal of the juvenile birds begins.

EVOLUTIONARY RELATIONSHIPS

In his revision of grouse genera, Short (1967) merged the monotypic genus *Bonasa* with the Eurasian genus *Tetrastes*, which contained two species of "hazel grouse." The two Eurasian species lack neck ruffs but otherwise are very similar to the ruffed grouse, and Short considered that, of the two, the European hazel hen (*T. bonasia*) is nearest to the North American ruffed grouse. The habitat of this bird in Europe is one of mixed hill woodlands and thickets, and it is especially prevalent in aspen and birch, which strongly suggests a common ecological niche. The winter diet of the Siberian hazel hen (*T. b. sibiricus*) consists of from 70 to 80 percent buds and catkins of birches (Dement'ev and Gladkov, 1967), which further attests to the strong ecological similarities of these species and certainly suggests a common evolutionary descent.

In contrast to the ruffed grouse, the hazel hen is apparently monogamous and forms a pair bond that lasts at least until hatching and sometimes beyond. An additional behavioral difference is that the male display consists largely of whistling calls (Dement'ev and Gladkov, 1967). There is no drumming display, but apparently an aerial display involving the whirring of wings does occur (Hjorth, 1970). It would seem that the evolution of a promiscuous mating system, development of nonvocal acoustical signals rather than reliance on vocal whistles, and the correlated ritualization of aerial display flights into a sedentary drumming display all occurred after the separation of ancestral ruffed grouse stock.

Short (1967) concluded that the nearest relationships of the genus *Bonasa* (in the broad sense) are with *Dendragapus* and that the former genus probably arose from pre-*Dendragapus* stock. I agree that modern species of *Dendragapus* or *Tetrao* probably represent the nearest living relatives of *Bonasa*.