THE CONDOR

VOLUME 58 SEPTEMBER-OCTOBER, 1956 NUMBER 5

OBSERVATIONS ON A SOOTY GROUSE POPULATION AT SAGE HEN CREEK, CALIFORNIA

By ROBERT S. HOFFMANN

In recent years there has been considerable interest in two separate aspects of the biology of Blue Grouse (*Dendragapus*). The first of these is the controversy concerning their taxonomy. The genus is widely distributed in the coniferous forests of the western states and consists of two groups of races recognized by some as separate species: the *fuliginosus* group, or Sooty Grouse, along the Pacific coast, and the *obscurus* group, or Dusky Grouse, in the Great Basin and Rocky Mountain areas. Originally these two groups were placed under the name *Dendragapus obscurus* on the basis of supposed intergradation (Bendire, 1892:41, 44, 50). The work of Brooks (1912, 1926, 1929) and Swarth (1922, 1926), however, led to their separation in the fourth edition of the A.O.U. Check-list (1931) into coastal and interior species. This split stood until the publication of the 19th Supplement to the A.O.U. Check-list (1944) when, following Peters (1934), *D. fuliginosus* and its subspecies were replaced under *D. obscurus*. Although at that time some doubt was still expressed about the correctness of this merger (Grinnell and Miller, 1944:113), intergradation in northern Washington and southern British Columbia between the races *fuliginosus* and *pallidus* has now been reported by several authors (Munro and Cowan, 1947:89; Carl, Guiguet, and Hardy, 1952:86; Jewett, Taylor, Shaw, and Aldrich, 1953:200).

The taxonomy of these grouse must rest upon the fact of intergradation between the two groups of races. Regardless of the final taxonomic disposition of the Blue Grouse, there are certain biological contrasts between the *fuliginosus* and *obscurus* groups which remain worthy of emphasis, even if they are not considered to justify specific separation of the racial groups.

The second aspect of Blue Grouse biology to arouse recent interest relates to the nature of population fluctuations exhibited by these birds. Until fairly recently it has been widely assumed that their populations also undergo the regular, almost periodic, fluctuations in density that have been described for other species of grouse—the "grouse cycle" or "ten-year cycle." Lately, the assumption that Blue Grouse are cyclic has been questioned (Bendell, 1955*a*), and the matter has not been settled to date.

A study of the coastal form, or Sooty Grouse (*D. fuliginosus*), in the vicinity of Sage Hen Creek, Nevada County, California, from December, 1951, until June, 1955, provided observations on a small, relatively isolated population. Comparison of the behavior and density fluctuations in this population with previous descriptions of other populations is pertinent to the current problems of taxonomy and population fluctuations in the genus *Dendragapus*.

BEHAVIOR OF THE SAGE HEN CREEK POPULATION

The local study area (fig. 1) consists of the basin enclosing three headwater tributaries of Sage Hen Creek, at an altitude of about 7000 feet. The area, of about one-half square mile, is partly isolated from the surrounding ridges by dense brush fields of

Ceanothus and *Arctostaphylos*. White firs (*Abies concolor*) are the predominant trees, with a few red firs (*Abies magnifica*), Jeffrey pines (*Pinus jeffreyi*) and western white pines (*Pinus monticola*). A dense riparian growth of willows (*Salix* sp.) and alders (*Alnus tenuifolia*) occurs along the streamside, and aspens (*Populus tremuloides*) and lodgepole pines (*Pinus contorta*) are present on moist soil sites.

Migration.—Various authors (Anthony, 1903; Grinnell, Bryant, and Storer, 1918; Marshall, 1946; Wing, 1947; Bendell, 1955*b*) agree that Blue Grouse usually perform an altitudinal migration from their winter habitat in the coniferous forests on the high

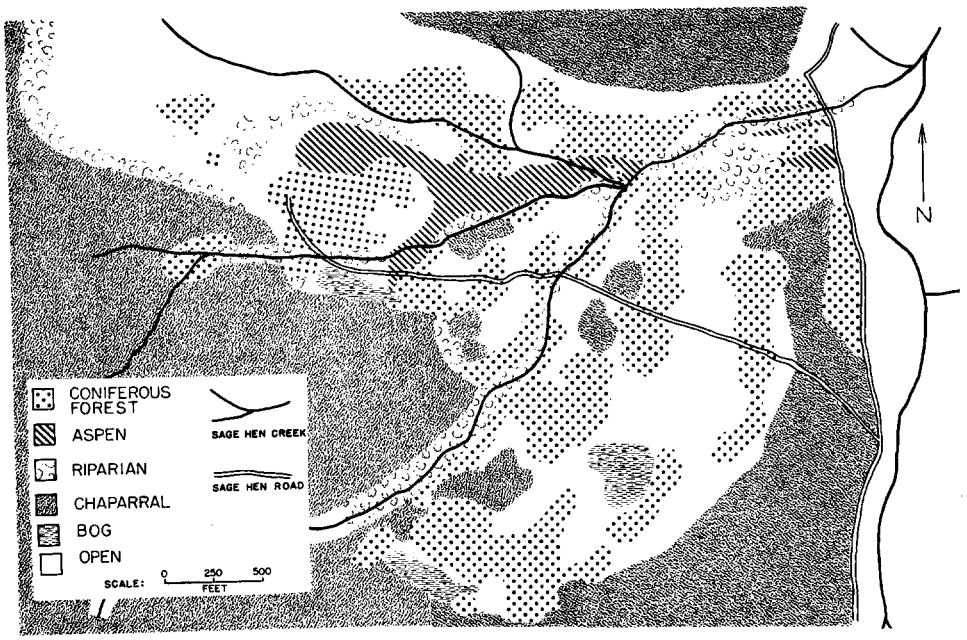


Fig. 1. Map of study area showing vegetation types around headwaters of Sage Hen Creek, Nevada County, California; map prepared from United States Forest Service aerial photograph (C.D.J. 12–56, 6–27–39) and ground survey.

ridges down to their breeding range in lower, often more open country. This movement occurs in early spring (March or April), prior to any breeding activity, and is accomplished in a relatively short period of time. After breeding, males begin to move back upslope in July, and the hens and chicks follow in August and September. Normally, then, breeding and winter ranges are completely separated.

This was not true of the population at Sage Hen Creek. Although only observational evidence is available, it is fairly certain that the Sooty Grouse wintering on the study area were the same ones which bred there. No extensive altitudinal migration took place, and although movements of 500 to 600 yards probably occurred, from a winter roost site on a ridge down to a nesting site in the aspens near the creek, these distances are within the magnitude of the normal daily range of the grouse. Other populations of Blue Grouse have been reported to reside in one area throughout the year, either at high altitudes (Swarth, 1926:83; Johnson, 1929:292–293; Schottelius, MS; Jewett *et al.*, 1953:197) or low (Jewett *et al., loc. cit.*).

Flocking.—A second aspect of the behavior of the local population which is at variance with the reported behavior of other Blue Grouse concerns flock formation. The

normal social organization in both *fuliginosus* and *obscurus* groups is that of a small flock throughout most of the year. Following the decline of courtship behavior, adult males associate in bands of five to six birds during their uphill migration to the winter range (Fowle, MS; Wing, Beer, and Tidyman, 1944:439; Caswell, MS). Similarly, a shuffling and combining of hens and their broods into loose flocks occurs later in the summer, prior to the uphill migration (Wing, Beer, and Tidyman, *op. cit.*:435 ff.; Bendell, 1955*b*:377). On the winter range of *D. obscurus pallidus,* Caswell (MS) reports flocks of six to ten grouse, including adult males, as frequent. Bendire (1889:33), Munro (1919:66), and Beer (1943:34) have also remarked on winter groups.

No flocks of grouse, excluding hens with broods, were noted in the course of the study of the Sage Hen Creek population. In a total of 43 encounters involving 51 grouse, 35 solitary birds and 8 pairs were seen. Of the pairs, four consisted of a male and female, one of two males, and three of unknown sex. While these observations are biased by the fact that most of the field work was done in the spring and early summer when solitary behavior is normal, I feel that the data indicate a real behavioral difference in this population.

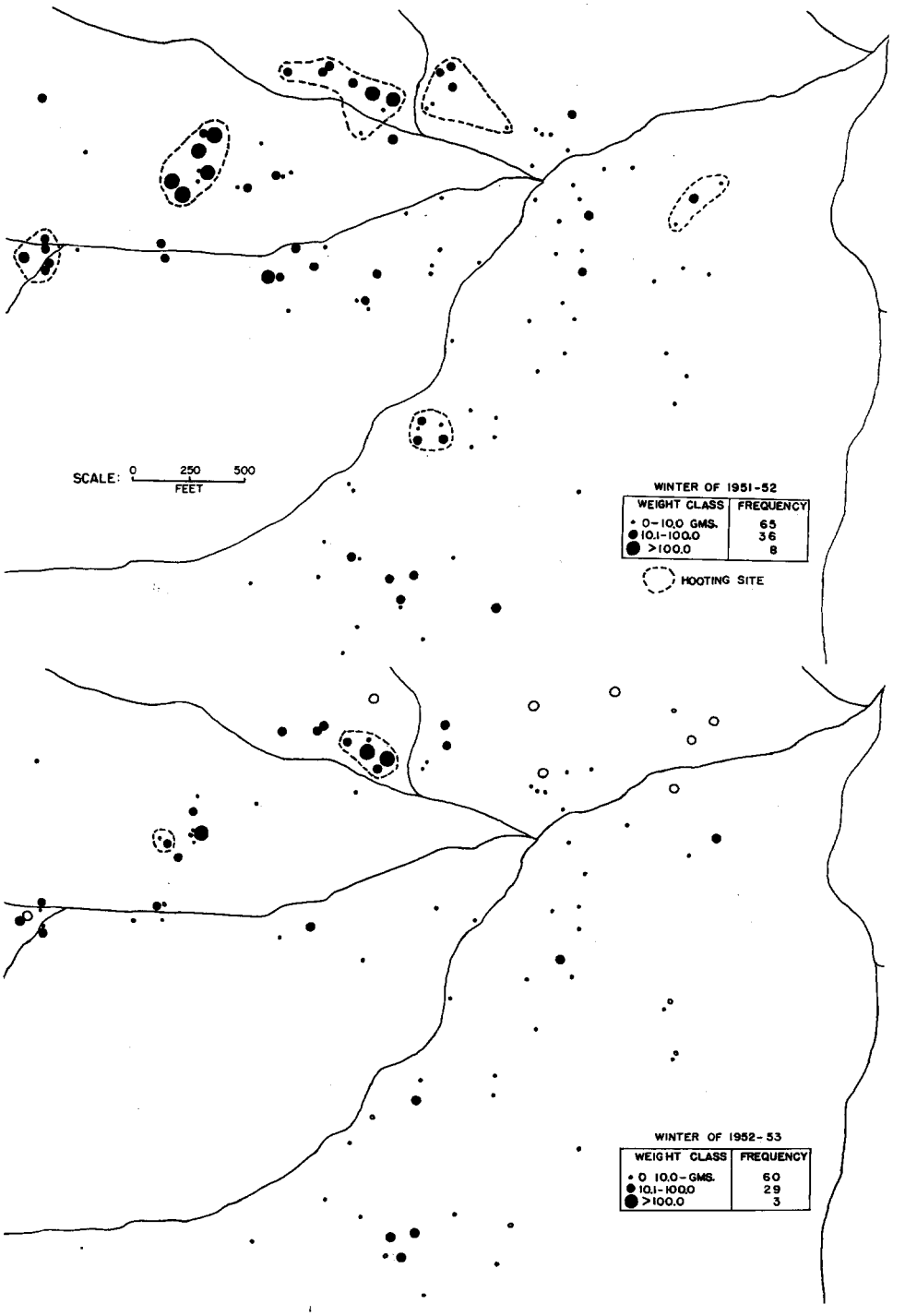
Breeding behavior.—Observations on behavior of the Sooty Grouse in the spring breeding period were made in the course of obtaining a tally of displaying male birds. The count of these hooting males consisted merely of following the sound produced by a displaying cock until he was located and then noting his position on a map. In some instances the bird could not actually be seen, in which event approximate locations were noted. The whole study area was covered for a series of ten days in 1952, seven days in 1953, five days in 1954, and five days in 1955.

Figure 2 shows the occurrence of hooting male grouse in the springs of 1952, 1953, and 1954. Each "hooter" was apparently restricted to a small area, in which he could be found displaying almost every day throughout the courtship period. From these observations it is inferred that adult male grouse in this population are territorial during the courtship period, as were the Sooty Grouse cocks described by Bendell (1955*b*:369).

The volume, frequency, and cadence of hoots of displaying cocks at Sage Hen Creek is the same as that described by earlier workers for the *fuliginosus* group (Bent, 1932: 105; Grinnell, Bryant, and Storer, 1918:548; Edson, 1925:227). Usually a hooting bird was situated near the top of a white fir, but occasionally he might be found hooting from a Jeffrey or lodgepole pine. Two separate birds were observed hooting from the ground on May 17, 1953.

In 1952, the first hooting was heard on the study area on May 10. In the month prior to this date, full days were spent on the area on April 11, 19, 20, and May 1, 4, 9. Negative observations on these dates indicate that active hooting began in the second week of May. Hooting seems to have begun earlier in the springs of 1951, 1953, and 1954. A. S. Leopold (unpublished field notes) found hooting in full swing after the middle of April in 1951. My field notes record no hooting on April 12, 1953, and active hooting on April 28, 1953, so hooting must have begun after mid-April in that year. In 1954, cock grouse were hooting on April 28, but no observations are available for the period prior to this date. It is concluded that hooting began at least by the last week of April in that year.

The factor that most obviously correlates with the onset of hooting and the courtship period in the male grouse is the persistence of snow cover in the spring. The years 1951, 1953, and 1954 approached the average in this respect, with snow cover on the study area disappearing around the first of May. In contrast, a snow cover was present for a full month longer in 1952, following a winter of record snowfall. This abnormally persistent snow cover may have inhibited the normal onset of courtship behavior in the


SCALE: 0 250 500
FEET
WINTER OF 1951-52
WEIGHT CLASS
FREQUENCY
0-10.0 GMS.
65
10.1-100.0
36
>100.0
8
HOOTING SITE
WINTER OF 1952-53
WEIGHT CLASS
FREQUENCY
0 10.0-GMS.
60
10.1-100.0
29
>100.0
3

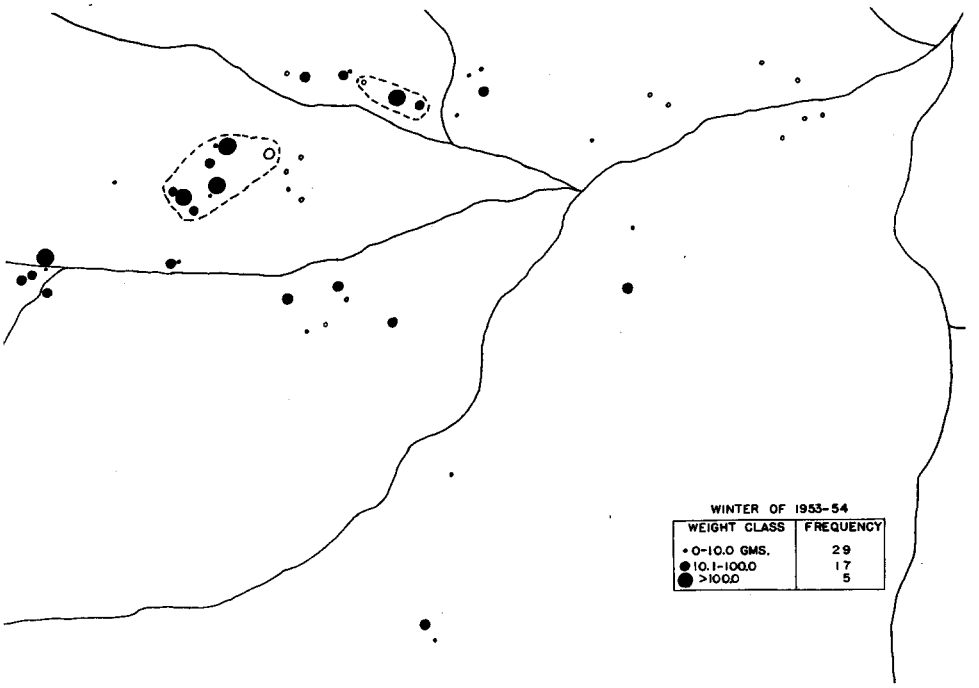


Fig. 2. Distribution of winter roost sites and hooting territories of breeding male grouse in the following spring, for 1951–52, 1952–53 (see opposite page), and 1953–54. Weight class of roost sites refers to total weight of droppings collected at that site (see text). Open circles in last two years indicate roost sites not occupied in previous winter.

male grouse, perhaps by delaying the normal transition to spring foods from the winter diet of fir needles.

The date of hooting cessation also appeared to be unusual in 1952. No hooting was heard after May 30, although a great deal of time was spent in the field. In contrast, prolonged, regular hooting was heard throughout June of the next two years, and even as late as July 6, 8, and 27, 1953, and July 4 and 5, 1954. No reason for the abrupt termination of hooting in 1952 is apparent.

Winter behavior.—As has been well described by previous authors (Belding, 1892; Grinnell, Bryant, and Storer, 1918; Beer, 1943; Stewart, 1944; Marshall, 1946), Blue Grouse ascend coniferous trees of several kinds with the approach of winter and remain in these trees most of the time, feeding on their needles, until the melting of the snow cover in spring once more allows them to obtain food from the ground. White fir is by far the most favored roost tree in the Sage Hen Creek area. The distribution of winter roost sites in three winters is indicated in figure 2. A comparison of this distribution with the map of the study area in figure 1 shows that the heaviest winter use of the fir tree roosts was concentrated in the area surrounding the only extensive aspen stand. This pattern held for all three winters, in both high and low population densities.

Several explanations for this correlation suggest themselves. One is the presence of permanent springs in the aspen grove that tend to remain free of snow throughout much of the winter, thus providing a source of accessible water and perhaps a few food plants. A second possibility is that the grouse favor the southern exposure of this slope.

It is apparent from figure 2 that some roost sites are utilized to a much greater

degree than are others (Beer, 1943:34; Wing, 1947:506). However, only a small part of the total white fir on the areas was used for roosts. The factors influencing this selection on the part of the grouse are not known. No obvious correlation existed between size or dispersion of the trees and degree of winter use. A further point is that each grouse probably roosts in a number of trees in the course of the winter and does not remain in just one or a few trees. Caswell (MS) also found this to be true in Idaho.

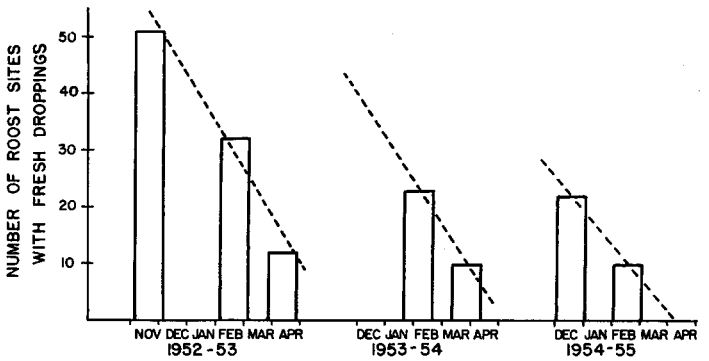


Fig. 3. Trend in numbers of occupied roost sites on the study area during the winters of 1952–53, 1953–54, and 1954–55. A roost site was considered occupied if fresh grouse droppings were visible on the snow surface beneath the roost trees.

Figure 3 indicates that a progressive decline in the number of roost sites in current use occurred in the course of each winter. This decline might be due to progressive winter mortality among the grouse, although there is no evidence to support this conjecture.

Discussion.—The morphological differences between the *fuliginosus* and *obscurus* groups of the genus *Dendragapus* have been thoroughly discussed by earlier authors. These differences include well-developed, orange gular air sacs coupled with a loud hoot during courtship in the coastal Sooty Grouse and less fully developed, purplish gular sacs that produce a soft hoot in the inland Dusky Grouse. Tail shape is also reported to be different in the two groups (Brooks, 1912:252, 1926:282–283; Swarth, 1922:204, 1926:80), as is coloration of the downy chicks (Moffitt, 1938).

Behavioral differences between the two groups of Blue Grouse have not been emphasized to the same extent as morphological differences. Brooks (1926:282–283) mentioned that in his experience the Dusky Grouse (subspecies *richardsoni*) "always utters [its courtship] hooting from the ground," whereas Sooty Grouse hoot from "high up in a coniferous tree." This difference seems to hold in the majority of cases (Wing, 1946: 157), but evidence from the present study and others (Edson, 1925:228; Johnson, 1929:292) shows that the Sooty Grouse, at least, may deviate from its usual behavior and occasionally hoot from the ground.

Another behavioral difference between the two groups for which some evidence is available concerns territoriality in the breeding males. Bendell (1955*b*:369) is the first author to give an adequate description of such territorial behavior, for the subspecies *fuliginosus*. He found that in a population on Vancouver Island the adult males were strongly territorial when hooting. Adult males always returned to the same territory each spring, but if a male failed to return, his place was taken by a new male, or the adjacent male expanded his own territory. Fowle (MS) also came to the conclusion that Sooty Grouse were territorial when hooting, on the basis of general observations in the same area. In contrast to this well-marked territorialism among displaying males of the

fuliginosus group, Schottelius (MS) and Caswell (MS) found that no territorialism was apparent in hooting males of the race *Dendragapus obscurus pallidus*. Schottelius reported as many as seven males in simultaneous display on a two-acre "hooting area." However, this conclusion was based on observational evidence alone.

These several behavioral differences may be correlated with the different habitat preferences of the two groups in the breeding season. The North American grouse that indulge in communal courtship display are *Centrocercus, Tympanuchus, Pedicoecetes,* and, as noted above, there may be at least a tendency toward this in the *obscurus* group of *Dendragapus*. Such communal display is performed on the ground in open country. In the *fuliginosus* group of *Dendragapus,* and in *Canachites* and *Bonasa,* the courtship display is solitary and is performed in denser cover, usually from a tree or log.

Throughout the summer, the *fuliginosus* group, along the humid Pacific coast, in general inhabits fairly dense cover of aspen groves and meadow edges adjacent to dense coniferous forests. The *obscurus* group of the more arid interior, on the other hand, often moves out onto quite open bunch grass and sagebrush-grass areas to breed. Brooks (1926:283) first emphasized this difference. Corroboration of his opinion is found in the comments of many authors (Anthony, 1903:26; Saunders, 1914:130; Lee, 1936: 122; Wing, Beer, and Tidyman, 1944:429; Marshall, 1946:43, 46, 50; Wing, 1947: 508; Schottelius, MS; Jewett, *et al.,* 1953:193–195; Caswell, MS, for the *obscurus* group; and Grinnell, Bryant, and Storer, 1918:547; Dawson, 1923:1591–1595; Burleigh, 1929:509; Bent, 1932:106; Gabrielson and Jewett, 1940:210; Grinnell and Miller, 1944:113–116; and Jewett, *et al.,* 1953:198, for the *fuliginosus* group). A possible exception to this generalization is the nesting behavior of the subspecies *obscurus* in Colorado and Wyoming, since Rockwell (1908:161), Neilson (1926:99), Skinner (1927:210, 213), and Bent (1932:91) consider the nesting range to be within the area of aspen and conifer timber.

The population of Sooty Grouse at Sage Hen Creek, although inhabiting the eastern edge of the range of the *fuliginosus* group, on the arid, Great Basin side of the Sierra Nevada, seems, in its behavior, to resemble *D. f. fuliginosus* from the humid coastal forests rather than any member of the *obscurus* group from the Great Basin. Displaying males were found day after day and year after year at the same hooting sites, and each site was well separated from adjoining sites. From these observations, territorial behavior is inferred. Furthermore, almost all hooting was done from trees.

Previous mention has been made of the atypical, non-migratory habits of the population. A downhill migration along Sage Hen Creek for a distance of about eight miles would bring the population from its present year-round range to an area of sagebrush-bunch grass along the lower part of the creek and the Little Truckee River. This open terrain of sagebrush and bunch grass is similar to the summer range used by some populations of Dusky Grouse, but it is not typical of breeding areas used by Sooty Grouse. Whether or not the grouse population in the Sage Hen basin was ever migratory is not known. It is conceivable that altitudinal migration might have taken place in the past, when, according to the testimony of old residents of the area, the grouse population was denser. The present lack of flocking behavior in the Sage Hen Creek population might also be associated with low population density. On the other hand, the absence of pronounced altitudinal migration could be a behavioral character relatively fixed genetically in this population.

POPULATION FLUCTUATIONS IN BLUE GROUSE

In spite of a voluminous literature on the general topic of grouse "cycles," very little is known concerning population fluctuations in the Blue Grouse. Leopold (1933:58)

and Wing (1947:510) both state that Blue Grouse are cyclic, but they do not cite any specific data. Bendell (1955*a*:221) has recently introduced a proper note of caution by questioning the uncritical assumption that Blue Grouse populations must be cyclic merely because other grouse exhibit this pattern of population change.

Historical evidence for cycles in Blue Grouse.—By following the procedure of two recent investigators (Buckley, 1954; Williams, 1954), an indication of the trends in

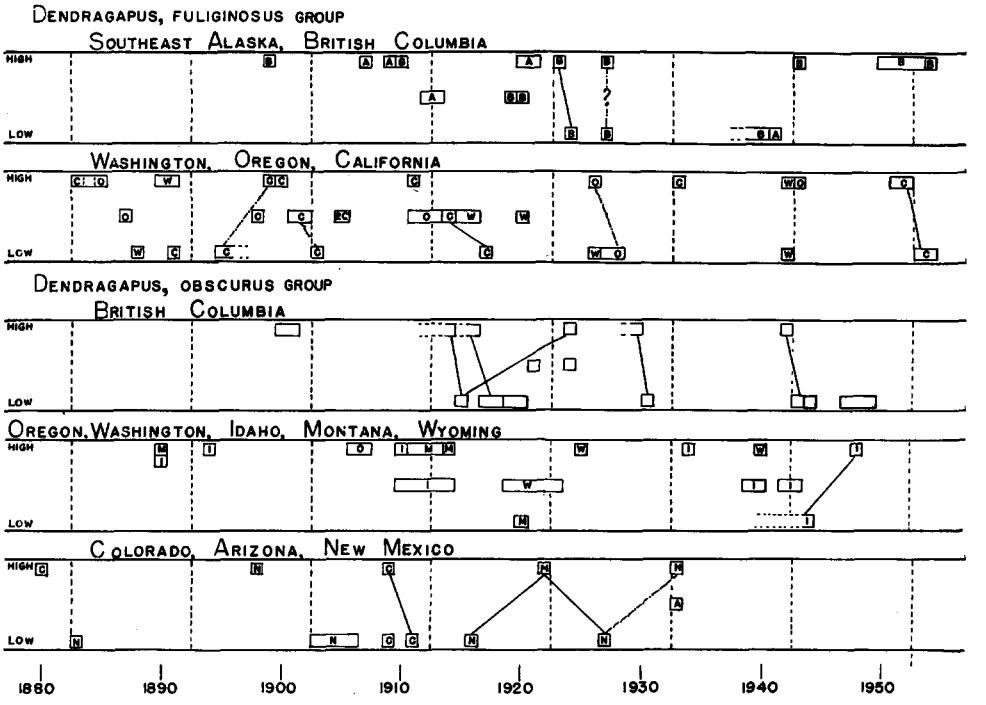


Fig. 4. Relative abundance of Blue Grouse, 1880–1954, plotted according to whether literature records indicated high ("abundant," "numerous"), medium ("fairly common," "not uncommon"), or low ("scarce," "rare") population density. Letters within the symbols indicate the locality (A—Alaska or Arizona, B—British Columbia, C—California or Colorado, I—Idaho, M—Montana, N—New Mexico, O—Oregon, W—Washington or Wyoming). Vertical dashed lines indicate years ending in "3"—the approximate peak year for the grouse-hare cycle. Solid lines connect symbols in instances of a definite population change described in the reference; broken lines connect symbols in instances of successive references to the same area by the same or different authors. See appendix, pp. 334–337.

Blue Grouse populations may be found. All references (see appendix) in the literature to the Blue Grouse which contained a concrete statement on relative numbers were plotted by species and by area (fig. 4). It is apparent that the data are too incomplete to warrant more than the most tentative conclusions. There are, however, several good descriptions of high grouse populations which suddenly were reduced.

Thus, for the race *D. o. obscurus,* Warren (1912:91) comments on the scarcity of both this species and the White-tailed Ptarmigan (*Lagopus leucurus*) in 1911 in north-central Colorado, where they had been common in 1909. Also Bailey (1928:197), discussing this race in New Mexico at the southern extreme of its range, indicates a fluc-

tuation in numbers from a low in 1916 through a high in 1922 and back to a low in 1927. By 1933, both Blue Grouse and ptarmigan had attained high numbers again (A. Starker Leopold, unpublished field notes).

To the north, in British Columbia, a series of observers documented the fall and rise in numbers of *D. o. richardsoni*. In the West Kootenay District, Kelso (1926:701) reports the species "common . . . until 1914, when its numbers were sadly reduced by a disease. It is regaining its former numbers [in 1924–25]." Ruffed Grouse were similarly affected. Mailliard (1932:274) states that *D. o. richardsoni* was "reported to have been quite common, but in 1928 grouse were very scarce" in the Kootenay Valley, about 50 miles from the area observed by Kelso. Ruffed Grouse were "even more scarce" than Blue Grouse. In another part of British Columbia, at Okanagan Landing, Munro (1919: 65) states that *D. o. richardsoni* was "abundant in normal years" but that their "numbers [were] greatly reduced during the past two years [1917–18]." In a later paper (1923:72) he indicates Ruffed and Sharp-tailed grouse suffered a decline at the same time, while snowshoe hares disappeared in 1915. Finally, Ferrie (*fide* Williams, 1954: 10) indicates that following a peak in 1942, populations of Blue Grouse and Sharp-tailed Grouse "crashed" in 1943.

Fewer convincing accounts of "crash" declines in the *fuliginosus* group exist in the literature. Howell (1917:186) says that *D. f. sierrae* in Mono County, California, was "well represented" in 1914, and very rare in 1917. Racey (1926:321) describes a situation at Alta Lake, British Columbia, in which the grouse (*D. f. fuliginosus* and *Canachites franklini*) were abundant in 1923 and almost gone in 1924. Fowle (MS) presents evidence from the annual reports of the British Columbia Game Commission which suggest a series of ten-year cycles from 1903 to 1943 in *D. f. fuliginosus* and snowshoe hares. Finally, observations at Sage Hen Creek, Nevada County, California, since 1951, indicate that there was an abrupt decline in *D. f. sierrae* in this area in 1952.

The Sage Hen Creek population.—Major objectives at the outset of the present study were to devise some way of determining the relative abundance of Sooty Grouse from year to year. Two techniques were employed, as previously mentioned: a count of displaying male grouse in the spring, and an analysis of the winter roost sites of the grouse. The validity of a census of displaying males rests upon the territorial behavior exhibited by adult male Sooty Grouse during the courtship period. The number of roost sites used in the course of a winter, and the amount of droppings accumulated beneath, presumably is dependent on the number of grouse that winter in an area. Granting this assumption, a count of winter roost sites and a measurement of the amount of droppings at these sites can serve as an index of the overwintering grouse population.

The method by which hooting males were counted has been described. Roost sites were located simply by cruising the entire study area, mapping and marking each tree or group of trees which was found to have grouse droppings. This was done primarily in early spring, when the melting snow pack made the droppings most conspicuous. It is estimated that well over 90 per cent of all the roost sites were found by this method, and certainly none of the major sites was overlooked.

The next step was to take samples of the droppings. The distribution of droppings beneath the roost trees was not random, that is, the droppings were grouped into discrete piles here and there beneath the trees of the site. Since it was desirable to determine approximately the total amount of droppings deposited each winter, a program of systematic sampling was adopted. At each site the number of dropping groups was first determined by inspection, then a circular area of one square meter was circumscribed around each area of greatest dropping concentration. The number of samples thus varied with the site, but the same number was always taken each year, allowing comparison

from year to year. The air-dry samples were then weighed to give a figure for the intensity of use for each roost site.

The results of these two index techniques are plotted on maps (fig. 2) for each year. Six cock grouse were found displaying in the spring of 1952, and a total of 109 roost sites was used in the preceding winter. The total weight of droppings collected was 2676 gms. In the spring of 1953, the number of hooting males decreased to two, each of which was in a site which had held a hooting cock in 1952. The number of roost sites used in the preceding winter decreased to 92, and the total dropping weight to 1548 gms. The spring of 1954 found two hooting males, again occupying the same two sites as 1953. The number of roost sites declined further to 51, but total dropping weight increased slightly, to 1595 gms. In the spring of 1955 no count of winter roost sites was made, but two hooting males were again present in the same two sites occupied by displaying males in the previous two years.

Table 1

Total Weight of Grouse Dropping Samples under Winter Roosts

Weight classes	Frequency of Class in 1952		Frequency of Class in 1953		Frequency of Class in 1954	
0– 9.9 gms.	65		59		29	
10– 19.9	17		15		3	
20– 29.9	7		3		3	
30– 39.9	5		5		4	
40– 49.9	0		2		1	
50– 59.9	2		1		1	
60– 69.9	3		2		3	
70– 79.9	1	7	0	5	1	6
80– 89.9	1		1		1	
90– 99.9	0		1		0	
100–109.9	0		0		1	
110–119.9	2		0		0	
120–129.9	0	4	0	1	0	3
130–139.9	1		1		1	
140–149.9	1		0		1	
150–159.9	0		1		1	
160–169.9	0		0		0	
170–179.9	2	4	0	2	0	2
180–189.9	1		1		0	
230–239.9	1		0		0	
250–259.9	0		0		1	
Total number of roosts used	109		92		51	
Total weight of droppings from all winter roosts	2676 gms.		1548 gms.		1595 gms.	

When the dropping samples are grouped by weight classes (table 1), it is seen that a significant decline in the frequency of the higher classes occurred between 1952 and 1953, and that between 1953 and 1954 the significant decrease was in the two lowest classes. Both hooting and roost site indices indicate a sharp decline in numbers of Sooty Grouse in 1952 and subsequent maintenance of a low population level (see also fig. 3). Since there is no open season in California, hunting was not a factor in the decline.

The occurrence of a sparse population of snowshoe hares (*Lepus americanus taho-*

ensis) in the Sage Hen Creek basin afforded the opportunity of determining whether the crash of the presumed ten-year cycle in Sooty Grouse also affected the hares, as would be expected. At the same time that winter grouse droppings were being sampled, the number of hare droppings present in each sample was recorded in the spring of 1952 and 1953. The average number of droppings thus represents an index of relative abundance of snowshoe hares in the preceding winter. In 1952 there was an average of 11.21 droppings per sample for 227 samples. In 1953, an average of 6.41 droppings per sample was present in 163 samples. The decline in average number of hare droppings per sample between 1952 and 1953 parallels the sharp decline in the Sooty Grouse population over this same period and suggests that the sparse snowshoe hare population may have declined synchronously with the grouse.

The evidence available on grouse and hare populations at Sage Hen Creek thus points to a sharp decline in numbers of both species in 1952. This decline falls into the schedule of the hypothetical ten-year cycle, which predicted a peak around 1951–53, followed by "crash" decline of continental grouse and hare populations (Rowan, 1950).

The accumulated data seem to indicate that Blue Grouse *may* resemble other species of northern grouse in exhibiting a ten-year cycle. As in these other grouse, a tendency for Blue Grouse populations to fluctuate synchronously with other grouse in a given area, and with snowshoe hare populations, is indicated by various comments in the cited literature. Local variations in the time of the crash decline are also apparent from the observations in British Columbia (Munro, 1919, 1923; Kelso, 1926).

One further point should be made with regard to "cycles." Some evidence suggests that population fluctuations in Blue Grouse, and perhaps other grouse, are less pronounced in the humid coastal forests bordering the north Pacific than in the interior. Buckley (1954:338) states that grouse, ptarmigan and snowshoe hare populations in southeastern Alaska are apparently relatively stable. Bendell (1955*a*:200, 221) found a population of Sooty Grouse at stable density on their breeding range from 1950 through 1953. In contradiction to this, Fowle (MS) documented a regular ten-year cycle in Sooty Grouse in coastal British Columbia, but he found that after 1935 the populations did not fluctuate markedly. He attributed the relative stability to changed habitat conditions on the summer range resulting from widespread forest fires and subsequent development of a favorable vegetational succession. It is possible that the stability noted by Buckley and Bendell is a fairly recent development, although perhaps not necessarily due to the causes suggested by Fowle.

ACKNOWLEDGEMENTS

I wish to thank Dr. A. Starker Leopold for much advice and guidance in the course of this study. Dr. Frank A. Pitelka gave very helpful criticism of the manuscript. Joseph G. Hall, S. Kent Carnie, Glenn Flittner, Richard Gard, and Albert Jones, and my wife, Sally Hoffmann, assisted in many phases of the field work. The following manuscripts were kindly made available to me by loan: Caswell, E. B., a preliminary study on the life history and ecology of the blue grouse in west-central Idaho, Univ. Idaho Thesis, 1954; Fowle, C. D., the sooty grouse on its summer range, Univ. Brit. Columbia Thesis, 1944; Schottelius, B. A., studies on the blue grouse . . . in the Methow Valley of Washington, State College of Washington Thesis, 1951.

Acknowledgement is also made for the financial assistance given to the University of California for the Sagehen Creek Project by the Max C. Fleischmann Foundation of Nevada in 1953. The facilities and equipment provided there under its grant were of great value in carrying out the present study. Dr. Paul R. Needham extended courtesies to me in the course of my field work at the Sage Hen Creek Experiment Station.

Financial assistance for the study came from National Science Foundation fellowships in 1952–53 and 1954–55. The Annie M. Alexander fellowship of the University of California provided support in 1953–54.

SUMMARY

Observations on the behavior of a small, semi-isolated population of Sooty Grouse at Sage Hen Creek, California, are compared with published observations on other populations. The grouse at Sage Hen Creek differ from most previously described populations in that they do not perform a seasonal altitudinal migration and in that no flocking behavior has been observed. These differences may be a reflection of low population density.

Evidence presently available points to pronounced differences in courtship behavior between the Dusky Grouse (*obscurus* group) of the interior and the Sooty Grouse (*fuliginosus* group) along the Pacific coast. These differences appear to be correlated with differences in summer range chosen by the two groups. The tendency toward communal display with no obvious territoriality is found in Dusky Grouse on open summer range, whereas solitary display and strongly developed territoriality occurs among Sooty Grouse on more wooded summer range. Although the grouse at Sage Hen Creek occupy the extreme eastern portion of the range of the *fuliginosus* group, the population has maintained the pattern of courship display and breeding habitat preference found in the main populations of the *fuliginosus* group. They show no tendency to resemble the *obscurus* group of the Great Basin in these respects, although the topography and vegetation of the Sage Hen drainage makes such a shift in habits theoretically possible.

The occurrence of displaying male grouse in the spring, and of winter roost sites, was determined at Sage Hen Creek for the period from the winter of 1951–52 through the spring of 1955. These two indices of population density suggest that the numbers of Sooty Grouse on the study area, and the numbers of snowshoe hares as well, declined in late 1952. This decline is perhaps of the same nature as other declines in Blue Grouse populations described in the literature.

LITERATURE CITED

American Ornithologists' Union Committee.
1931. Check-list of North American birds. Fourth edition (published by the Union, Lancaster, Pa.).

Anthony, A. W.
1903. Migration of Richardson's grouse. Auk, 20:24–27.

Bailey, F. M.
1928. Birds of New Mexico (New Mexico Dept. Fish and Game).

Bendire, C. E.
1889. Notes on the habits, nests, and eggs of *Dendragapus obscurus fuliginosus*, the sooty grouse. Auk, 6:32–39.
1892. Life histories of North American birds with special reference to their breeding habits and eggs. U. S. Nat. Mus. Spec. Bull. No. 1, 446 pp.

Beer, J.
1943. Food habits of the blue grouse. Jour. Wildl. Manag., 7:32–44.

Belding, L.
1892. Food of the grouse and mountain quail of central California. Zoe, 3:232–234.

Bendell, J. F.
1955*a*. Disease as a control of a population of blue grouse, *Dendragapus obscurus fuliginosus* (Ridgway). Canad. Jour. Zool., 33:195–223.

1955*b*. Age, breeding behavior and migration of sooty grouse, *Dendragapus obscurus fuliginosus* (Ridgway). Trans. Twentieth N. Amer. Wildl. Conf.:367–381.

Bent, A. C.
1932. Life histories of North American gallinaceous birds. U. S. Nat. Mus. Bull. 162, 490 pp.

Brooks, A.
1912. Some British Columbia records. Auk, 29:252–253.
1926. The display of Richardson's grouse, with some notes on the species and subspecies of the genus *Dendragapus*. Auk, 43:281–287.
1929. On *Dendragapus obscurus obscurus*. Auk, 46:111–113.

Buckley, J. L.
1954. Animal population fluctuations in Alaska—a history. Trans. Nineteenth N. A. Wildl. Conf.:338–357.

Burleigh, T. D.
1929. Notes on the bird life of northwestern Washington. Auk, 46:502–519.

Carl, G. C., Guiquet, C. J., and Hardy, G. A.
1952. A natural history survey of the Manning Park area, British Columbia. Occ. Pap. B. C. Prov. Mus. No. 9, 130 pp.

Dawson, W. L.
1923. The birds of California (South Moulton Company, San Francisco) 4 vols.

Edson, J. M.
1925. The hooters of Skyline Ridge. Condor, 27:226–229.

Gabrielson, I. N., and Jewett, S. G.
1940. Birds of Oregon (Oregon State College, Corvallis).

Grinnell, J., Bryant, H. C., and Storer, T. I.
1918. The game birds of California (University of California Press, Berkeley).

Grinnell, J., and Miller, A. H.
1944. The distribution of the birds of California. Pac. Coast Avif. No. 27:1–608.

Howell, A. B.
1917. Condition of game birds in east-central California. Condor, 19:186–187.

Jewett, S. G., Taylor, W. P., Shaw, W. T., and Aldrich, J. W.
1953. Birds of Washington state (University of Washington Press, Seattle).

Johnson, R. A.
1929. Summer notes on the sooty grouse of Mount Rainier. Auk, 46:291–293.

Kelso, J. E. H.
1926. Birds of the Arrow Lakes, West Kootenay district, British Columbia. Ibis, ser. 12, 2:689–723.

Lee, O. S.
1936. Occurrence of young dusky grouse in an alfalfa field. Condor, 38:121–122.

Leopold, A.
1933. Game management (Charles Scribner's Sons, New York).

Mailliard, J.
1932. Birds and mammals from the Kootenay valley, southeastern British Columbia. Proc. Calif. Acad. Sci., ser. 4, 20:269–290.

Marshall, W. H.
1946. Cover preferences, seasonal movements, and food habits of Richardson's grouse and ruffed grouse in southern Idaho. Wilson Bull., 58:42–52.

Moffitt, J.
1938. The downy young of *Dendragapus*. Auk, 55:589–595.

Munro, J. A.
1919. Notes on some birds of the Okanagan Valley, British Columbia. Auk, 36:64–74.
1923. Winter bird life at Okanagan Landing, British Columbia, 1917 and 1918. Canad. Field-Nat., 37:70–74.

Munro, J. A., and Cowan, I. McT.
1947. A review of the bird fauna of British Columbia. B. C. Prov. Mus. Spec. Publ. No. 2, 285 pp.

Neilson, J. A.
1926. Bird notes from Wheatland, Wyoming. Condor, 28:99–102.
Peters, J. L.
1934. Check-list of birds of the world. Vol. 2 (Harvard University Press, Cambridge).
Racey, K.
1926. Notes on the birds observed in the Alta Lake region, B. C. Auk, 43:319–325.
Rockwell, R. B.
1908. An annotated list of the birds of Mesa County, Colorado. Condor, 10:152–180.
Rowan, W.
1950. The coming peak of the ten-year cycle in Canada. Trans. Fifteenth N. Amer. Wildl. Conf.: 379–383.
Saunders, A. A.
1914. The birds of Teton and northern Lewis and Clark counties, Montana. Condor, 16:124–144.
Skinner, M. P.
1927. Richardson's grouse in the Yellowstone Park. Wilson Bull., 39:208–214.
Stewart, R. E.
1944. Food habits of blue grouse. Condor, 46:112–120.
Swarth, H. S.
1922. Birds and mammals of the Stikine River region of northern British Columbia and southeastern Alaska. Univ. Calif. Publ. Zool., 24:125–314.
1926. Report on a collection of birds and mammals from the Atlin region, northern British Columbia. Univ. Calif. Publ. Zool., 30:51–162.
Warren, E. R.
1912. Some north-central Colorado bird notes. Condor, 14:81–104.
Wetmore, A., *et al.*
1944. Nineteenth supplement to the A.O.U. Check-list. Auk, 61:441–464.
Williams, G. R.
1954. Population fluctuations in some northern hemisphere game birds (Tetraonidae). Jour. Anim Ecol., 23:1–34.
Wing, L.
1946. Drumming flight in the blue grouse and courtship characters of the Tetraonidae. Condor, 48:154–157.
1947. Seasonal movements of the blue grouse. Trans. Twelfth N. Amer. Wildl. Conf.: 504–511.
Wing, L., Beer, J., and Tidyman, W.
1944. Brood habits and growth of 'blue grouse.' Auk, 61:426–440.

APPENDIX

References to Relative Numbers of Blue Grouse. Consult literature cited for publication and pagination of those references that are cited by year only.

Fuliginosus Group

Southeastern Alaska, British Columbia

Bailey, A. M. Auk, 44:1927:1–23, 184–205. Southeastern Alaska: In 1920–21, "common."

Bendell (1955*a*). Vancouver Island, B.C.: In 1950–53, "extremely high."

Bishop, L. B. N. Amer. Fauna No. 19, 1900:47–100. Yukon region: In 1899, "told that [sooty] grouse were common"; *Canachites* "reported as common"; *Bonasa* "rare at Lower Lebarge . . . common near Rampart City."

Brooks, A. Auk, 40, 1923:217–224. Porcher Island, B.C.: In 1920, "common" [implies they would be abundant, except for bald eagles].

Cook, F. S. Canad. Field-Nat., 61, 1947:131–133. Queen Charlotte Islands, B.C.: In 1942, "rather scarce in recent years."

Darcus, S. J. Canad. Field-Nat., 44, 1930:45–49. Queen Charlotte Islands, B.C.: In 1927, "very common on Graham Island . . . almost exterminated on Langara Island by domestic cats."

Grinnell, J. Univ. Calif. Publ. Zool., 5, 1909:171–264. Southeastern Alaska: In 1907, "common."

Hardy, G. A. Prov. Mus. Nat. Hist. Anthrop., Rept. for 1954, 1955:24–63. Vancouver Island: In 1943 and 1950–54, "common."

Jewett, S. G. Murrelet, 23, 1942:67–75. Southeastern Alaska: In 1941, though reported as "fairly common, . . . not a single grouse seen."

Patch, C. A. Canad. Field-Nat., 36, 1922:101–105, 133–136. Queen Charlotte Islands, B.C.: In 1919, "fairly common."

Racey (1926). See text. Large increase in number of great horned owls noted during grouse decline.

Swarth, H. S. Univ. Calif. Publ. Zool., 7, 1911:9–172. Southeastern Alaska: In 1909, "abundant."

Swarth, H. S. Univ. Calif. Publ. Zool., 10, 1912:1–124. Vancouver Island, B.C.: In 1910, "common at most of the points visited."

Willett, G. Condor, 16, 1914:71–91. Southeastern Alaska: In 1912–13, "hardly . . . abundant [but] very generally distributed." Goshawks common in 1912, very scarce in 1913.

Washington, Oregon, California

Anthony, A. W. Auk, 3, 1886:161–172. Washington County, Oregon: In Feb., 1884–June, 1885, "abundant." *Bonasa* "abundant."

Barlow, C. Condor, 2, 1900:103–110. Pyramid Peak Area, California: In 1900, "hear quite commonly."

Barlow, C., and Price, W. W. Condor, 3, 1901:151–184. Placerville–Lake Tahoe area, California: "not common at any point" prior to 1900 [1895?–1900].

Burdick, A. W. Condor, 46, 1944:238–242. Northern Cascade Mountains, Washington: In 1942, "abundant." *Canachites* "common."

Burleigh (1929). Coastal northwestern Washington: In Sept., 1919–June, 1920, "fairly plentiful." *Bonasa* "fairly plentiful."

DeGroot, D. S. Condor, 36, 1934:6–9. Echo Lake, California: In 1933, "seemed to be unusually abundant."

Ferry, J. F. Condor, 10, 1908:30–44. Yollo Bolly Mountains, California: In 1905, "common in favorable localities."

Fisher, A. K. N. Amer. Fauna No. 7, pt. II, 1893:7–393. Southern Sierras, California: In 1891, "nowhere common." *Centrocercus* also scarce.

Gabrielson, I. N. Condor, 33, 1931:110–121. Rogue River Valley, Oregon: "not common, [but] more common in 1926 than in other years."

Howell (1917). See text.

Jewett, S. G. Condor, 18, 1916:74–80. Tillamook County, Oregon: In 1911–14, "fairly common." *Bonasa,* "not uncommon."

Jewett, Taylor, Shaw, and Aldrich (1953). Mount Adams, Washington: In July, 1942, "very scarce."

Johnson (1929). Mount Rainier, Washington: In 1926, "saw the Sooty Grouse seldom in other parts of its natural range," but fairly common around one camp ground.

Kellogg, L. Univ. Calif. Publ. Zool, 12, 1916:335–398. Northern coast ranges, California: In 1911, "abundant . . . . A farmer . . . complained that grouse were so numerous that they were injuring his young grain."

Kobbé, W. H. Auk, 17, 1900:349–358. Cape Disappointment, Washington: In 1898, "only one seen." *Bonasa* not "abundant."

Lawrence, R. H. Auk, 9, 1892:39–47. Grey's Harbor, Washington: In 1890–91, "common." *Bonasa* "common."

McAllister, T. H., Jr., and Marshall, D. B. Auk, 62, 1945:177–189. Lake County, Oregon: In 1943, "common."

Merriam, C. H. N. Amer. Fauna No. 16, 1899:1–169. Mount Shasta, California: In 1898, "fairly common."

Merrill, J. C. Auk, 5, 1888:139-146. Fort Klamath, Oregon: In Sept., 1886–Aug. 1887, "generally distributed, . . . but not abundant." *Bonasa* "common."

Rathbun, S. F. Auk, 33, 1916:357–370. Olympic Mountains, Washington: In 1915–16, "fairly common." *Bonasa,* "not common."

Ray, M. S. Auk, 20, 1903:180–193. Central Sierras, California: In 1901–02, "not uncommon."

Ray, M. S. Auk, 22, 1905:363–371. Central Sierras, California: In 1903, "one seen . . . a few heard [in June]."

Stone, W., and Bunnell, A. S. Proc. Acad. Nat. Sci. Phila., 56, 1904:576–585. Mount Sanhedrin, California: In 1899, "numerous."

Townsend, C. H. Proc. U. S. Nat. Mus., 10, 1887:159–241. Mount Shasta, California: In 1883–84, "common."

Obscurus Group

British Columbia

Brooks, A. Auk, 20, 1903:277–284. Cariboo District, B.C.: In 1900–01, "common." *Canachites* "abundant."

Ferrie (*fide* Williams, 1954:10). See text.

Kelso (1926). See text.

Mailliard (1932). See text. High juvenile mortality noted during grouse decline.

Munro (1919). See text. Decline attributed to "cold, wet springs and the ravages of an intestinal parasite."

Munro (1923). See text. During decline, broods were "unusually small although there has been a fairly dry hatching season."

Munro, J. A., Occ. Pap. B. C. Prov. Mus. No. 8, 1950, 90 pp. Creston region, B. C.: "Blue Grouse were scarce in 1947 and only slightly less so in 1948 and 1949." *Bonasa* "scarce both in 1947 and 1948."

Rand, A. L. Nat. Mus. Canad. Bull. No. 105, 1946, 76 pp. Yukon region, B. C.: In 1944, "not common."

Rand, A. L. Canad. Field-Nat., 64, 1950:214–220. Yukon region, B. C.: In 1919–20, "scarce and local." *Bonasa, Canachites,* and *Lagopus* apparently also scarce.

Swarth, H. S. Univ. Calif. Publ. Zool., 24, 1924:315–394. Skeena River, B. C.: In 1921 "in small numbers." *Bonasa* "abundant."

Swarth (1926). Atlin region, B. C.: In 1924, "fairly common at high altitudes." *Canachites* "ordinarily . . . a common species . . . but in 1924 . . . had declined in numbers to a point of actual scarcity."

Oregon, Washington, Idaho, Montana, Wyoming

Arvey, M. D. Condor, 51, 1949:98. Custer and Blaine counties, Idaho: "much more numerous [in 1948 than] in 1938–44." *Canachites* "abundant."

Burleigh, T. D. Auk, 38, 1921:552–565. Lincoln County, Montana: In 1920, "a scarce breeding bird." *Bonasa* "common."

Gabrielson, I. N. Auk, 41, 1924:552–565. Wallowa County, Oregon: "past four years [1919–23?], . . . common [but] not exceedingly abundant." *Bonasa* "very common."

Hand, R. L. Condor, 43, 1941:220–232. Shoshone and Clearwater counties, Idaho: "In August, 1934, 150 seen at one time."

Jewett, S. G. Auk, 26, 1909:5–9. Baker County, Oregon: In 1906–07, "abundant." *Bonasa* "common."

Jewett, S. G. Condor, 14, 1912:191–194. Saw-tooth Mountains, Idaho: In 1910, "common."

Marshall, W. H. Condor, 47, 1945:170–172. Elmore County, Idaho: In winters of 1938–39 and 1939–40, "rather common." *Bonasa* "fairly common."

Merriam, C. H. N. Amer. Fauna No. 5, 1891:1–108. South-central Idaho: In 1890, "abundant."

Neilson (1926). Laramie Peak, Wyoming: In 1925, "most common."

Richmond, C. W., and Knowlton, F. H. Auk, 11, 1894:298–308. South-central Montana: In 1890, "very common."

Rust, H. J. Condor, 17, 1915:118–129. Kootenai County, Idaho: In 1910–14, "fairly common." Bonasa, "more abundant during . . . 1914 than for many years past."

Saunders (1914). Teton, and Lewis and Clark counties, Montana: In 1911–13, "abundant."

Saunders, A. A. Condor, 17, 1915:109–115. Flathead Lake, Montana: In 1914, "really common."

Snyder, J. O. Auk, 17, 1900:242–245. In 1894, "abundant." *Bonasa* "commonly seen."

Wing, L. Murrelet, 25, 1944:3–8. Okanogan County, Washington: In 1940, "most abundant."

Yocom, C. F., and Yocom, I. G. Murrelet, 27, 1946:10–12. Kootenai County, Idaho: In 1943, "reported as rather common, yet we did not see any." *Bonasa,* "rather common."

Colorado, Arizona, New Mexico

Bailey (1928). See text.
Drew, F. M. Bull. Nuttall Ornith. Club, 6, 1881:85–91, 138–143. San Juan County, Colorado: In 1879–80, "common." *Lagopus,* "very common."
Henshaw, H. W. Auk, 2–3, 1885–86:326–333, 73–80. Upper Pecos River, New Mexico: In 1883, "not abundant, though generally distributed."
Huey, L. M. Wilson Bull., 48, 1936:119–130. White Mountains, Arizona: In 1933, "not common."
Mitchell, W. I. Auk, 15, 1898:306–311. San Miguel County, New Mexico: In 1898, "common."
Rockwell, R. B., and Wetmore, A. Auk, 31, 1914:309–333. Golden, Colorado: In 1909, "not common."
Warren (1912). See text.

Museum of Vertebrate Zoology, University of California, Berkeley, California; current address, Department of Zoology, Montana State University, Missoula, Montana; January 24, 1956.