AUTUMN WEIGHTS OF BLUE GROUSE IN NORTH-CENTRAL WASHINGTON, 1954 TO 1963

FRED C. ZWICKEL, JAMES H. BRIGHAM, and IRVEN O. BUSS

Bird populations of North America vary geographically in body weight (Stoddard, 1931; Buss *et al.*, 1947; Mayr, 1956), and according to Timoféeff-Ressovsky (1940) and Salt (1963), become progressively heavier with increasing distance from their centers of distribution in major biogeographic regions. The adaptive significance of variation in body size is probably best expressed in Bergmann's Rule, which notes that body size is correlated inversely with ambient temperatures (Rensch, 1939; Salomonsen, 1955). Pitelka (1951) concluded that populations of the Scrub Jay, *Aphelocoma coerulescens*, followed Bergmann's Rule and also observed a correlation between small size and dense vegetation. These and numerous other studies indicate that there has been an interest in the adaptive significance of body size in birds, but that relatively few studies have focussed on its ecologic significance.

Bendell (1955) has presented an analysis of mean summer weights of Blue Grouse, *Dendragapus obscurus*, from Vancouver Island, and Boag (1965) has presented a comparison of weights of Blue Grouse from different areas of northwestern North America, again mostly from summer records. We have no knowledge of extensive published data on the autumn weights of Blue Grouse.

In the fall of 1954 we began recording weights of hunter-killed Blue Grouse of the race *D. o. pallidus*, at two widely separated checking stations in north-central Washington. We continued to take weights through 1963. The principal objectives of these checking stations were to gather data relative to harvests and population characteristics of the three forest grouse found here, that is, the Blue Grouse, the Spruce Grouse (*Canachites canadensis*), and the Ruffed Grouse (*Bonasa umbellus*). In the beginning, we hoped that annual trends in weight might provide information on annual population changes and give a greater insight into the biology of the Blue Grouse in this region. We now find that no correlations are apparent between mean weights and annual fluctuations in the fall populations and therefore feel it is appropriate to present the 2236 autumn weights that we have as a contribution toward an understanding of the biology of Blue Grouse. While there are certain weaknesses of sample size in these data, they do come from well-defined study areas and are not thus pooled data from large regions, as is so often the case in this type of analysis.

METHODS

Body weights were taken from grouse killed by hunters on week ends in September or early October. Since 1958 the hunting season has opened on the week end prior to 15 September and before that year, on the week end following 15 September. Weights were recorded to the nearest gram on triple beam balances. All birds were uneviscerated and had crops intact. Sex was determined as suggested by Caswell (1954), and age was determined by using a combination of shape of outer primary contours (the principal method used) and probing of the bursa of Fabricius. The data are analyzed by the following four sex and age classes: adult male, juvenile male, adult female, and juvenile female.

At the time of the hunting season in this region most yearling birds have completed their first postnuptial primary molt and cannot be distinguished from adults. A few still retain one juvenile primary, however, and can be recognized as yearlings, as in Ruffed Grouse (see Hale *et al.*, 1954). Unless otherwise noted, all yearlings have been pooled with adults, as distinguished from juveniles, but a short discussion will be presented on the weights of recognizable yearlings.

The two study areas are designated here as the Chumstick and Conconully areas. More birds were examined in the Conconully than in the Chumstick area because of differences in the road networks in the two regions. Annual comparisons are therefore more reliable for Conconully than for Chumstick.

DESCRIPTION OF AREAS

Both study areas are located along the eastern fringe of the Cascade Mountains. The Chumstick area comprises approximately 100 square miles of mountains that are bounded on the south by the Wenatchee River and on the north by the Entiat River. The Conconully area comprises approximately 100 square miles of mountains lying between the town of Conconully and the Methow River drainage. The two areas are about 75 airline miles apart, in a north–south direction. Chumstick is in the Cascade Mountain Province and Conconully in the Okanogan Highlands Province (Culver, 1936).

Elevations at which grouse hunting occurs in the Chumstick area range from approximately 1500 feet above sea level in Swakane Canyon, to 5840 feet above sea level at the top of Sugarloaf Mountain. The area straddles a long, steep ridge, Entiat Ridge, which runs from NW to SE and originates at the crest of the Cascade Mountains. In this area, the wheatgrass-bluegrass zone, the ponderosa pine zone, the Douglas fir zone, and the spruce fir zone can be identified (Daubenmire, 1946). These zones interdigitate with one another, change from slope to slope, and because of microclimates and edaphic variations often form a mosaic of vegetation types. The area is characterized by generally open south-facing slopes and ridge crests, with semi-dense to dense coniferous forests on north-facing slopes. Consequently, north-facing slopes are hunted mostly at lower elevations or along semi-open ridge crests whereas south-facing slopes are hunted more evenly. The area has about 20 inches of precipitation per year, most of which falls as snow in the winter.

The Conconully area is characterized by relatively smooth and less steep mountains (at lower elevations) and is dissected by many small streams flowing in all four cardinal directions. The hunting area ranges from around 1500 feet above sea level near Conconully, to 8275 feet above sea level at the top of Tiffany Mountain. There are five peaks in this area over 7500 feet high and eight other peaks which range between 4500 and 6000 feet. Much of the hunting is carried out along the lower ends of ridges leading to these peaks. The pattern of vegetation in the Conconully area shows considerable contrast to that in the Chumstick area. Because of a greater range in elevation, the sedgegrass or tundra zone is also present, in addition to all the other zones mentioned for Chumstick. The annual precipitation is about the same as at Chumstick but occurs mainly in spring and summer, during the growing season. Conconully is consequently more heavily forested than Chumstick, with most open areas occurring at lower elevations, on isolated south-facing slopes, along ridge crests, or in the tundra zone.

Land use within the two areas is principally that of timber management, grazing of domestic stock (mostly cattle), recreation, and watershed management. Because of the more gentle terrain in the Conconully area, grazing is more intensive and more evenly distributed than at Chumstick.

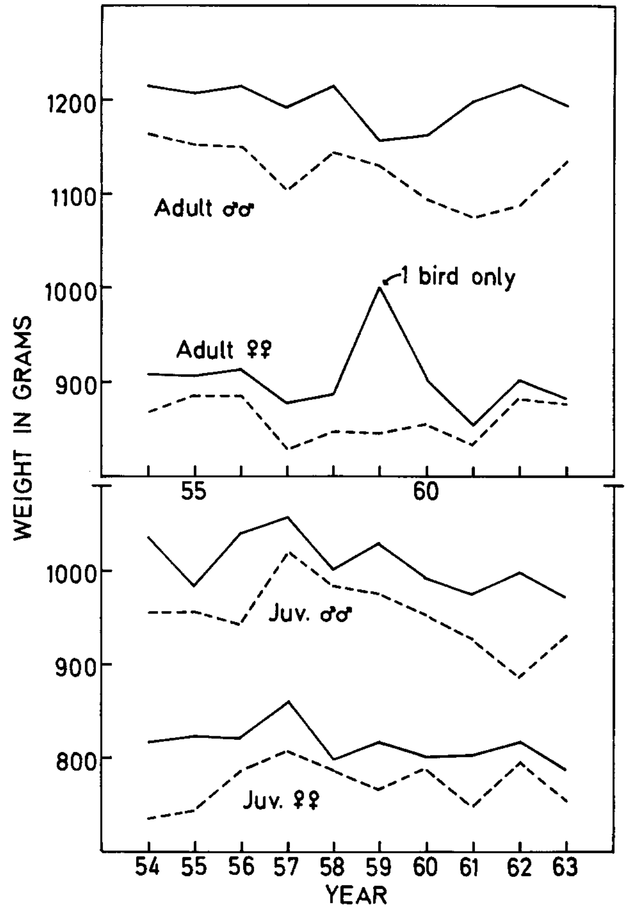

Figure 1. Mean annual weights of Blue Grouse at Chumstick (dotted line) and Conconully (solid line). Adults and yearlings are combined as "adults."

RESULTS

Weight comparisons between areas. A comparison of the annual mean weights for the different categories at the two areas is presented in figure 1 (data in table 1). Mean annual weights at Conconully, in all sex and age classes, are greater than those at Chumstick. Individual t tests between areas (for annual pairs of means within the different sex and age categories) show statistical significance in some cases but not in others. Although significance is not always indicated, the trend is clear, with all 40 of the annual means at Conconully being greater than those at Chumstick. The lack of significance in most cases is considered to be a result of the sample sizes involved in the annual comparisons and is not thought to invalidate the conclusion that Blue Grouse are heavier at Conconully than at Chumstick.

Although the annual weight comparisons between areas are not always statistically significant, the pooled means between areas, for the 10-year period (table 1), are significantly different for all sex and age classes (adult males, $t = 7.01$, $P <$

TABLE 1
MEAN ANNUAL WEIGHTS OF BLUE GROUSE RECORDED AT THE CHUMSTICK AND CONCONULLY CHECKING STATIONS, 1954 TO 1963
(Yearlings are combined with adults. Weights are in grams.)

	Males				Females			
	Adults		Juveniles		Adults		Juveniles	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean
Chumstick								
1954	20	1164	31	955	15	869	34	735
1955	4	1151	10	956	6	884	16	743
1956	13	1150	29	942	10	886	16	787
1957	6	1101	30	1020	5	829	31	808
1958	4	1145	13	984	5	849	21	789
1959	7	1130	13	976	6	848	19	768
1960	13	1095	13	951	15	854	25	789
1961	6	1076	17	928	7	832	21	749
1962	8	1089	21	887	9	882	28	796
1963	6	1132	15	930	6	879	13	755
Mean	87	1128	192	955	84	863	224	773
SE		10		11		11		6
Conconully								
1954	53	1215	63	1035	62	909	67	817
1955	53	1208	69	982	74	907	87	822
1956	29	1214	38	1040	37	912	41	821
1957	21	1191	44	1058	25	879	51	860
1958	34	1215	101	1000	36	888	92	799
1959	2	1158	4	1029	1	1000	5	818
1960	14	1161	29	991	24	902	55	800
1961	19	1199	54	976	26	855	67	801
1962	27	1217	45	999	21	901	55	818
1963	20	1195	36	971	20	882	48	787
Mean	272	1207	483	1005	326	898	568	813
SE		5		5		4		3

0.001; juvenile males, $t = 18.07$, $P < 0.001$; adult females, $t = 3.95$, $P < 0.001$; and juvenile females, $t = 6.09$, $P < 0.001$). It is thus apparent that Conconully birds are heavier in the fall than Chumstick birds. The pooled means at Chumstick range from 94 to 96 per cent of those at Conconully, within the different sex and age classes.

Another factor apparent in table 1 is that juvenile females are nearer adult weight than are juvenile males. Expressed as percentages, these are as follows:

Mean weight of juvenile males as a percentage of that of adult males for Chumstick is 84 per cent and for Conconully is 83 per cent.

Mean weight of juvenile females as a percentage of that of adult females for Chumstick is 89 per cent and for Conconully is 91 per cent. This difference can be explained in two possible ways: (1) a similar absolute growth rate but different mean adult weights in the two sexes, or (2) a faster relative growth rate in juvenile females than in juvenile males. Other data which we have on the stage of molt and depth of bursae from these birds indicate the latter explanation to be the most prob-

TABLE 2
MEAN WEIGHT OF FEMALE BLUE GROUSE AS A PER CENT OF THE MEAN WEIGHT OF MALES
(Pooled means for the 10-year period.)

	Chumstick	Conconully
Adults	77	75
Yearlings	78	75
Juveniles	81	81

able; that is, that juvenile females approach maturity earlier than juvenile males. Koskimies (1958) reported for Blackgame (*Lyrurus tetrix*) and Capercaillie (*Tetrao urogallus*) in Finland that juvenile females were nearer adult weight in the fall than were juvenile males, thus agreeing with the findings reported here.

Koskimies has also presented data showing a large sexual dimorphism, based on weight, in the Blackgame and Capercaillie. His data indicate that in the autumn adult female Blackgame are approximately 75 per cent of the weight of the adult male, and adult female Capercaillie are approximately 48 per cent of the weight of the adult male. A similar analysis of our data is presented in table 2. These data indicate little difference in this parameter between areas or between adults and yearlings. The slightly higher percentages for juveniles are a result of the more advanced development of juvenile females over juvenile males, as noted above. These data suggest that the Blue Grouse is more like the Blackgame than the Capercaillie in this particular attribute.

Weight comparisons among years. As noted earlier, no correlations were observed among mean annual weights in any sex or age class, or indicated production in different years. Analysis of variance tests of the annual mean weights in the different categories (over the 10-year period) are presented in table 3. In all cases the mean weights of juveniles vary significantly among years; adults do not in three cases and do in one case (adult females at Conconully). Apparently there are differences in

TABLE 3
ANALYSIS OF VARIANCE TESTS OF THE DIFFERENCES OF ANNUAL MEAN WEIGHTS OF BLUE GROUSE IN FOUR CATEGORIES DURING A 10-YEAR PERIOD

	f Value	Significant at $P \leqslant 0.05$
Adult males		
Chumstick	1.04	No
Conconully	0.64	No
Juvenile males		
Chumstick	4.44	Yes
Conconully	3.73	Yes
Adult females		
Chumstick	0.31	No
Conconully	2.58	Yes
Juvenile females		
Chumstick	2.47	Yes
Conconully	3.58	Yes

TABLE 4
MEAN WEIGHTS OF ADULT BLUE GROUSE AS COMPARED WITH THOSE OF RECOGNIZABLE YEARLINGS AT CHUMSTICK AND CONCONULLY CHECKING STATIONS—POOLED DATA FOR 1954 TO 1963
(Weights are in grams.)

	Adults	Yearlings
Chumstick		
Males		
No.	76	11
Mean	1136	1069
SE	10	32
Females		
No.	63	21
Mean	875	830
SE	7	36
Conconully		
Males		
No.	246	27
Mean	1212	1157
SE	5	18
Females		
No.	252	74
Mean	905	872
SE	4	7

the mean weights of juveniles among years, but there are usually no differences in the mean weights of adults among years.

The mean weights of juveniles, in both sexes, generally follow parallel trends at the two areas over the period of study (fig. 1). Exceptions to this trend are probably the result of inadequate samples in some years. The generally consistent trends between years, in both sexes and at both areas, suggest a common cause. These variations are probably the result of annual variations in the peak of hatching and annual variations in the opening date of the hunting season. For instance, the generally lower weights for juveniles in recent years correlate with earlier season openings. At the same time the high juvenile weights indicated for 1957, while coming in a year of high production, correlate with an early hatch (Standing, 1960) and a postponement of the opening date of the hunting season because of fire hazard. The size of samples in some years makes a year-by-year analysis of these data of doubtful value. We can offer no explanation for the very low weight of juvenile males at Chumstick in 1962, a year when the sample size does not appear to be inadequate.

Weights of yearlings. The sample sizes from known yearling birds are too meager to justify an annual treatment. Nevertheless, the mean weights of yearlings are intermediate between those of adults and juveniles in 25 of 34 possible comparisons at the two different areas and in the different sex and age classes. A comparison of the mean weights of adults (which include unrecognizable yearlings) to the mean weights of recognizable yearlings—pooled data for 10 years—is presented in table 4.

In all cases the mean weights of yearlings are statistically different than those of adults ($P < 0.01$). Unless recognizable yearlings represent only small individuals, which is a possibility, these data suggest that yearling birds have not yet reached full adult weight by their second autumn. The large overlap in range of weight between the two age classes is probably largely a result of most yearlings being included with the adults. The mean weights of adult birds, as compared to yearlings, therefore, are a minimum weight for birds two and one-half years and older.

DISCUSSION

We have presented an analysis of 2236 autumn weights of Blue Grouse which were collected over a 10-year period. These weights were obtained incidental to the collection of other data which we considered of relevance to our studies of population dynamics and hunter harvests. Since no experimentation has been involved in these studies, we can only offer suggestions for interpreting the results that are given. The small sample sizes in some years preclude definitive conclusions from the analyses of the annual records. We feel, however, that the samples are adequate to establish certain points.

It is obvious that Blue Grouse in the Conconully area are heavier in the fall than those in the Chumstick area. This difference in weight correlates with the following apparent differences between the two areas:

At Conconully: (1) a more northern latitude; (2) a less rugged terrain; (3) a deeper soil type; (4) a higher spring and lower winter precipitation; (5) as a result of (3) and (4), generally denser vegetation; (6) a wider range of elevation and, consequently, a wider range of vegetative types; (7) a more even, and more intense, livestock use; (8) in most years, a lower production of young per adult female (to be documented in another paper).

The birds in the Chumstick and Conconully areas are not considered racially distinct as both are included in the race *pallidus* (see Aldrich, 1963). Thus, racial origin, as suggested by Koskimies (1958) for differences in weights between areas that he reported for Blackgame and Capercaillie, would not seem to explain adequately these differences. One might suspect that nutrition is involved in these differences in view of the differences in soil depth, terrain, and vegetative types between the two areas; yet, the heavier livestock use and lower annual production at Conconully would seem to counter this argument. The two most probable explanations for the difference between areas seem to be: (1) These populations are on a racial cline in weight, or, (2) These populations represent ecotypes (both within a single race) which are reacting to specific, and probably complex, environmental conditions within their respective ranges. Whether such adaptations or reactions have significance in the population dynamics of this species is a question that cannot be answered at this time.

We do not have sufficient data on the breeding densities of the two study areas during this period. Hunter harvests, however, suggest that the densities of breeding birds have not varied markedly. As noted earlier, annual production has shown variations among years that do not correlate with variations in the mean weights of any sex or age class. Since annual production has differed and the mean annual weight of adults has generally not differed, variations in production are not correlated with variations in the autumn weight of adults. Since no correlations were observed between autumn age ratios and weights of juveniles, there is no evidence for any cause-and-effect relationship here. This latter finding suggests that annual variations in the summer survival of chicks are not associated positively with annual variations in growth, thus agreeing with an earlier report by Zwickel (1965).

The more rapid apparent growth rate in female than in male Blue Grouse agrees with generally accepted views on earlier maturity of females in a number of species of vertebrates. The close agreement in the amount of sexual dimorphism in weight between Blue Grouse and Blackgame, as compared with the Capercaillie, suggests that this may be an important parameter to consider in studies of the phylogeny of the tetraonids.

SUMMARY

Body-weight data were collected over a 10-year period from 2236 hunter-killed Blue Grouse in two areas of north-central Washington. Differences in mean weights were found between the two areas in all sex and age categories. These differences are thought to be a result of either a racial cline in weight between the two areas or ecotypic responses to the two environments. The mean weights of adults were found not to vary annually (with one exception), but the mean weights of juveniles did vary annually. No correlations were observed between annual mean weights in any sex or age category and autumn age ratios. With respect to weight, juvenile females appear to mature faster than juvenile males. The data suggest that the degree of sexual dimorphism in mean weights may be of value in studies of the phylogeny of the tetraonids.

ACKNOWLEDGMENTS

It would be inappropriate to try to single out all of the personnel of the Washington Department of Game, students from Washington State University, and others who have assisted with the collection of these data. Without their help these data could not have been collected and we greatly appreciate their contributions. We do feel we should express our gratitude to the following Department of Game personnel: Chester C. Ball, E. R. Brown, C. F. Martinsen, John R. Patterson, Clar Pratt, and J. C. Stout, all of whom supervised one or the other of the two checking stations for more than one year.

LITERATURE CITED

Aldrich, J. W. 1963. Geographic orientation of American Tetraonidae. J. Wildl. Mgmt., 27: 528–545.

Bendell, J. F. 1955. Age, molt and weight characteristics of Blue Grouse. Condor, 57:354–361.

Boag, D. A. 1965. Indicators of sex, age, and breeding phenology in Blue Grouse. J. Wildl. Mgmt., 29:103–108.

Buss, I. O., H. Mattison, and F. M. Kozlik. 1947. The Bobwhite Quail in Dunn County, Wisconsin. Wis. Cons. Bull., 12:1–8.

Caswell, E. B. 1954. A method for sexing Blue Grouse. J. Wildl. Mgmt., 18:139.

Culver, H. E. 1936. The geology of Washington. Part I, general features of Washington geology. State of Wash. Dept. of Cons. and Develop., Div. of Geol., Bull. 32.

Daubenmire, R. F. 1946. The life zone problem in the northern intermountain region. Northwest Sci., 20:28–38.

Hale, J. B., R. F. Wendt, and G. C. Halazon. 1954. Sex and age criteria for Wisconsin Ruffed Grouse. Wis. Cons. Dept., Tech. Wildl. Bull. 9, 24 pp.

Koskimies, J. 1958. Seasonal, geographical and yearly trends in the weight of Capercaillie (*Tetrao urogallus*) and Blackgame (*Lyrurus tetrix*) in Finland. Ornis Fennica, 35:1–18.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution, 10:105–108.

Pitelka, F. A. 1951. Speciation and ecologic distribution in American jays of the genus *Aphelocoma*. Univ. Calif. Publ. Zoöl., 50:195–464.

Rensch, B. 1939. Klimatische Auslese von Grössenvariaten. Arch. Naturgesch., N.F. 8:89–129.

Salomonsen, F. 1955. The evolutionary significance of bird migration. Kgl. Danske Videnskab. Selskab Biol. Medd., 22:1–62.

SALT, G. W. 1963. Avian body weight, adaptation, and evolution in western North America. Proc. XIII Intern. Ornithol. Congr., pp. 905–917.

STANDING, K. M. 1960. Factors in relation to population fluctuations in the Blue Grouse. Ph.D. thesis, Wash. State Univ.

STODDARD, H. L. 1931. The Bobwhite Quail. Its habits, preservation and increase. Charles Scribner's Sons, New York.

TIMOFÉEFF-RESSOVSKY, N. W. 1940. Zur Frage über die "Eliminationsregel": Die geographische Grössenvariabilität von *Emberiza aureola* Pall. J. Ornithol., 88:334–340.

ZWICKEL, F. C. 1965. Early mortality and the numbers of Blue Grouse. Ph.D. thesis, Univ. Brit. Columbia.

Department of Zoology, University of British Columbia, Vancouver, British Columbia; State of Washington Department of Game, Kelso, Washington; and Department of Zoology, Washington State University, Pullman, Washington, 18 December 1965.