VARIATIONS IN WEIGHT OF BLUE GROUSE (*DENDRAGAPUS OBSCURUS*)

J. A. REDFIELD[1]
Department of Zoology
University of Alberta
Edmonton, Alberta, Canada

The average weight of birds may vary between areas, seasons, years, sexes, and age-classes. Systematic variations in weight among areas have been noted and often agree with Bergmann's rule (Mayr 1963). Seasonal variations may be related to life history events such as breeding, migration, and molt (Hanson 1962; Lewin 1963; Richdale 1957). Annual variations in weight may be related to weather, population density, or nutrition (Breitenbach et al. 1963; Baldwin and Kendeigh 1938; Gates and Woehler 1968; Jenkins et al. 1963; Owen 1954; Richdale 1957). Finally, variations in weight among age-classes may be related to maturity.

Several papers have presented data on weight of Blue Grouse (*Dendragapus obscurus*) and these are briefly summarized below. Bendell (1955) concluded that weight of adult (2 years old and older) and 1-year-old grouse on Vancouver Island did not change in summer and that adults were heavier than yearlings of a corresponding sex. Boag (1965) studied grouse in the Rocky Mountains of Alberta and concluded that adult and yearling males do not change weight in summer, that adult females decline in weight during incubation in late May and early June, and that yearling females do not change weight like adults. Zwickel et al. (1966) showed significant differences in weight in autumn for two populations of Blue Grouse located about 130 km apart in north-central Washington state, but they generally found no significant differences in the weight of adults between years. All these authors have shown that females are lighter than males of a corresponding age-class.

These publications suggest that our understanding of the patterns of variations in weight of Blue Grouse is minimal and that the patterns may vary between subspecies. For four summers (1968–71) I collected weights of Blue Grouse from Vancouver Island, British Columbia, in conjunction with an intensive population study. The objectives of this paper are to examine these data by area, season, year, sex, and age-class. These data clarify and confirm some points about the seasonal patterns of weight of Blue Grouse, at least on Vancouver Island, and show some variable trends between areas and years. Ultimately, data such as these may be useful in understanding population trends, but it is only after variations in weight are elucidated that an approach can be made to the problem of weight and its effect on population dynamics or, conversely, the effect of population dynamics on weight.

STUDY AREAS

Grouse were sampled from populations near Port Alberni, Vancouver Island, B.C. (fig. 1). Four of the populations sampled came from the Ash River Valley, near Elsie Lake, 30 km NW of Port Alberni. The other populations were located W and SW of Port Alberni. By far the largest bulk of data was from birds on three intensively studied areas (areas 104, 107 and 108e). In fact, after 1968, only limited data were collected outside these areas.

The Port Alberni region is in the Coastal Western Hemlock Biogeoclimatic Zone (Krajina 1969). Average annual rainfall exceeds 250 cm. The terrain is mountainous, with elevations from sea level to about 2000 meters. Most of the region has been block-logged by clear cutting, and logging of the remaining mature forest is continuing. Nearly all birds were sampled on areas which were logged within the past 15 years. One area, Taylor River Burn, was mature forest that had been burned 7–9 months prior to obtaining the samples.

METHODS

Weights of grouse came from live birds captured in the months April through August and from birds shot by hunters in late August and early September. All grouse were weighed to the nearest 10 g with spring scales and all weights include crop and contents. Birds were classed as adult or yearling on the basis of the color and form of the outermost primaries.

Comparisons between areas were made by considering data from each area separately. Comparisons between seasons or years were made using data combined from areas 104, 107, and 108e. The number of grouse captured in any weekly or biweekly period was usually too small for meaningful comparisons. Likewise, the time of day grouse were captured was variable. Therefore, data were combined into monthly sampling periods for an analysis of seasonal trends. All birds, once captured, were individually marked, eliminating the necessity of recapture. Thus, all samples are for newly captured birds only.

[1] Present address: Institute of Animal Resource Ecology, University of British Columbia, Vancouver 8, British Columbia, Canada.

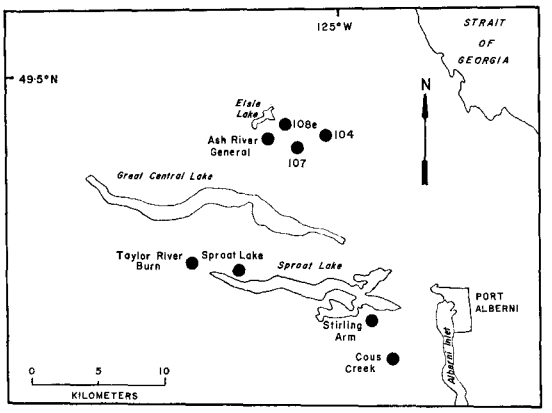

FIGURE 1. Locations of regions sampled near Port Alberni, B.C.

SOME ASPECTS OF THE LIFE HISTORY OF BLUE GROUSE WHICH MAY BE IMPORTANT IN AN ANALYSIS OF WEIGHT

Blue Grouse are found in mountainous areas of western North America. On Vancouver Island, they spend the winter in coniferous forests (Bendell and Elliott 1967) and in spring move to more open areas to breed. Densities of breeding birds in mature forests are low, but populations increase rapidly following logging or burning (Redfield 1972). After this initial increase, populations stabilize for a few years but then rapidly decline (Redfield et al. 1970). This decline seems to be caused by the increasing density of regenerating forests (Bendell and Elliott 1966).

Adult males migrate onto the breeding range in March and April and live solitarily on territories into July. By August, most adult males have left the breeding range. Yearling males come onto the breeding range in April and early May, but few hold territories and most have left by early July. Males do not assist females in construction of the nest, incubation, or care of the young. Factors which may affect weight of males in summer include territorial activity, molt, and changes in diet (King 1968).

Adult and yearling females migrate onto the breeding range in April and early May but do not appear to hold territories. Blue Grouse appear to be polygamous and breed in late April or May. Both adult and yearling females on Vancouver Island breed, and seasonal variations in weight of females may be related to egg formation, incubation, and raising of young. Nearly all hens attempt to nest (Zwickel and Bendell 1967), but in some years up to 50% may be unsuccessful. Most eggs hatch in June and chicks are nearly full grown by late September, when most grouse have left the breeding range. Females, like males, have changes in diet throughout summer (King 1968) and their primary molt starts shortly after chicks hatch. As with males, molt of the primaries is not complete by the time hens leave the study areas.

RESULTS

VARIATION BETWEEN AREAS

Variations in weight between populations might indicate differences in age-structure of populations or habitat suitability of different areas. Initially, one might assume that samples of grouse from regions within 50 km of each other would be relatively homogeneous. This analysis tests that idea.

In 1968, samples were obtained from all study areas. Since then, only the Ash River areas were sampled. These data are summarized in tables 1–4.

In 1968 and 1969, average weight of adult males varied significantly between areas, but in 1970 and 1971 it did not. In 1968, this variation was due to the low weights of males captured on Taylor River Burn; and in 1969, the Ash River General samples were heavier than those on the other Ash River study areas. In any given year the average weight of adult males did not vary between the three main Ash River study areas (104, 107, and 108e).

Sample sizes for yearling males are smaller than for adults and only in 1969 did average weight of yearlings vary between areas. The variation in 1969 was caused by heavier individuals in 104 as compared to 107 and 108e. No other variations in weight between areas were found among females.

The low weight of adult males on Taylor River Burn in 1968 may have been caused by an actual shortage of food since this area was literally rock and ashes in spring 1968. Since too few data for other sex- and age-classes in the Taylor River Burn were collected, no check of this suggestion can be made. The variation in weight of adult males in 1969 may have been caused by an age difference, since most of the males on the intensive study areas (104, 107, and 108e) were probably 2 years old while those on the general areas may have been 2 to several years old. The cause of the significant variation in weight of yearling males in 1969 is not known.

TABLE 1. Average weight (g) of adult male Blue Grouse on the study areas, 1968–71.

		Ash River				Taylor River Burn	Sproat Lake	Stirling Arm	Cous Creek
		104	107	108e	General				
1968	N	13	18		5	6	7	5	6
	$\bar{X}$	1342	1324	–	1365	1213	1329	1355	1375[a]
1969	N	7	6	19	6				
	$\bar{X}$	1209	1208	1262	1317[a]	–	–	–	–
1970	N	7	14	3					
	$\bar{X}$	1320	1318	1330	–	–	–	–	–
1971	N	2	19	8					
	$\bar{X}$	1205	1235	1249	–	–	–	–	–

[a] $P \leq 0.05$

TABLE 2. Average weight (g) of yearling male Blue Grouse on the study areas, 1968–71.

		Ash River				Taylor River Burn	Sproat Lake	Stirling Arm	Cous Creek
		104	107	108e	General				
1968	N	5	6			1	3	5	2
	$\bar{X}$	1095	1158	–	–	1100	1150	1145	1250
1969	N	12	13	10					
	$\bar{X}$	1133	1076	1072[a]	–	–	–	–	–
1970	N	5	10	4					
	$\bar{X}$	1054	1090	1045	–	–	–	–	–
1971	N	14	41	9					
	$\bar{X}$	1134	1131	1121	–	–	–	–	–

[a] $P \leq 0.05$.

TABLE 3. Average weight (g) of adult female Blue Grouse on the study areas, 1968–71 (brood hens only).

		Ash River				Taylor River Burn	Sproat Lake	Stirling Arm	Cous Creek
		104	107	108e	General				
1968	N	22	21		4		9		
	$\bar{X}$	862	872	–	894	–	878	–	–
1969	N	5	9	6	9		6		
	$\bar{X}$	825	826	800	835	–	788	–	–
1970	N	8	11	3	2				
	$\bar{X}$	849	837	840	838	–	–	–	–
1971	N	7	7	5					
	$\bar{X}$	812	806	822	–	–	–	–	–

TABLE 4. Average weight (g) of yearling female Blue Grouse on the various study areas, 1968–71 (brood hens only).

		Ash River				Taylor River Burn	Sproat Lake	Stirling Arm	Cous Creek
		104	107	108e	General				
1968	N	15	8				6		
	$\bar{X}$	825	823	–	–	–	824	–	–
1969	N	12	11	7	4		5		
	$\bar{X}$	817	815	817	763	–	790	–	–
1970	N	17	15	7					
	$\bar{X}$	779	755	753	–	–	–	–	–
1971	N	18	34	8					
	$\bar{X}$	799	786	774	–	–	–	–	–

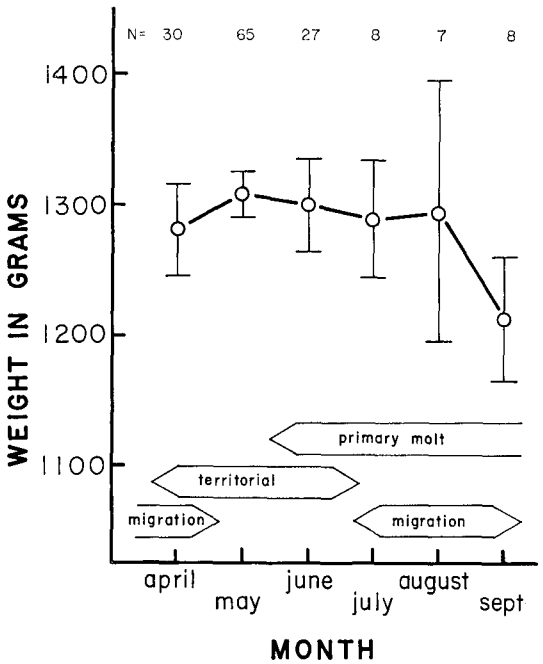

FIGURE 2. Average weight (± 2 SE) of adult male Blue Grouse captured during 1968–70. Bars below figure indicate the general duration of the major life history events.

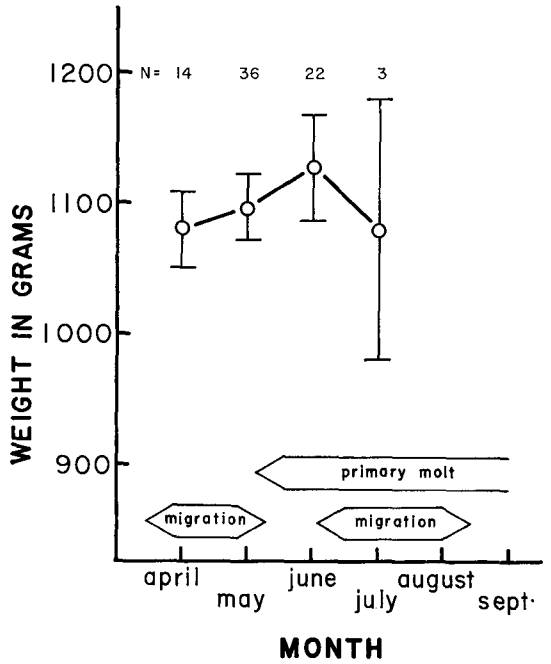

FIGURE 3. Average weight (± 2 SE) of yearling males captured during 1968–70.

VARIATIONS BETWEEN SEASONS

Comparisons of seasonal changes in weight are potentially useful and informative for ecological studies since these comparisons may (1) indicate fundamental physiological processes such as deposition of fat prior to winter; (2) suggest when periods of physiological or ecological stress occur; (3) indicate when food is in short supply; or (4) mark changes in reproductive conditions.

Because males migrate off the study areas earlier than females, data on seasonal variations in weight are more complete for females than males. Notwithstanding, the data are complete enough to indicate fundamental differences between males and females.

Weight of adult males did not change significantly from April–September in any year of this study (table 5). However, in all years the weight in September was lower than earlier in the year, suggesting a late summer loss in weight of males (fig. 2) even though this drop in weight in September was not significant. Koskimies (1958) found that males of both Blackgame (*Lyrurus tetrix*) and Capercaillie (*Tetrao urogallus*) maintained relatively constant weights from September–December. If this pattern is also found in adult male Blue Grouse, then weight of adult males is fairly constant from April–December. As will be pointed out later (see Variations Between Years), weight of adult male grouse varied from year to year and it seems likely that this variation was caused by seasonal variations in weight occurring during late winter (January, February, and March).

Weight of yearling males did not change significantly from April–July (table 6), but yearling males had a slight tendency to gain weight over summer (fig. 3). By July, most

TABLE 5. Average monthly weight (g) of adult male Blue Grouse, 1968–71.

	1968			1969			1970			1971		
	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$
April	–	–	–	21	1257	21	9	1341	25	11	1257	18
May	36	1345	14	20	1246	16	9	1303	20	13	1238	12
June	17	1300	26	5	1237	39	5	1326	17			
July	6	1300	29	2	1253	13	–	–	–	5	1189	16
Aug.	1	1370	–	5	1287	68	1	1250	–			
Sept.	3	1186	47	1	1175	–	4	1240	37			

TABLE 6. Average monthly weight (g) of yearling male Blue Grouse, 1968–71.

	1968			1969			1970			1971		
	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$
April	–	–	–	8	1088	12	6	1075	31	16	1132	4
May	10	1132	29	18	1083	17	8	1086	16	29	1114	6
June	10	1160	32	7	1145	33	5	1042	19	9	1143	6
July	1	1150	–	2	1045	65	–	–	–	8	1165	9

yearling males had left the breeding range and data for late summer are not available. We have no way, at present, to determine the age of newly captured birds older than 1 year of age, but due to the pattern of banding on the main study areas, it seems likely that most adults captured after 1968 were 2-year-olds. Adults in 1969, 1970, and 1971 were significantly heavier than yearlings in 1968, 1969, and 1970, respectively, suggesting that yearling males gain weight during their second winter of life.

The pattern of variation in weight of females is markedly different from that of males and although adult females are heavier than yearlings, both adults and yearlings have similar patterns of weight change through spring and summer (figs. 4 and 5, tables 7 and 8).

Weight of females increases significantly from April–May, followed by significant declines in June. In June and July females with broods (brood hens) are considered separately from those without broods (lone hens). Both brood hens and lone hens in June are lighter than hens in May and brood hens are also lighter than lone hens in June and July (table 9). The weight of brood hens increased slightly (not significant) in July and remained stable for the remainder of summer.

Weight of females fluctuates significantly throughout spring and summer. Thus, for comparisons between age-classes or between years, comparable periods must be used. Since weights of brood hens were stable, they were used for comparative purposes.

Yearling females were significantly lighter than adults. As with males, age-classes can not be separated beyond 1 year, but it also seems probable that yearling females gain weight during their second winter of life.

Koskimies (1958) noted that female Capercaillie and Blackgame gained weight during September and October before reaching a "normal winter weight." It seems likely that female Blue Grouse also gain weight in autumn or winter since adult females captured

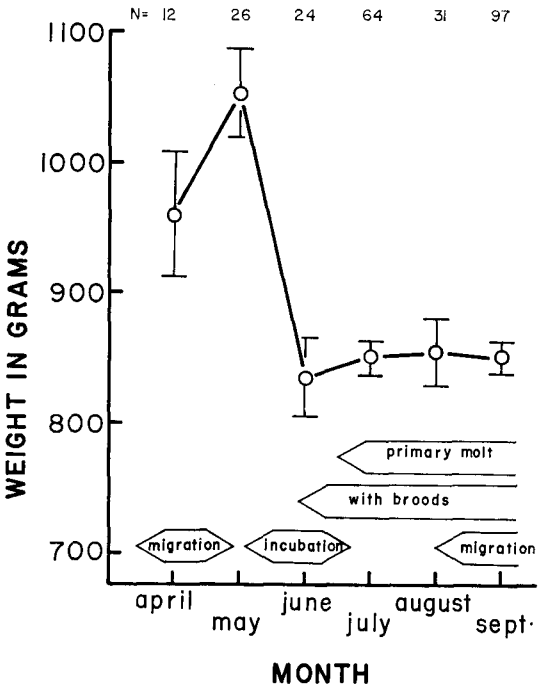

FIGURE 4. Average weight (± 2 SE) of adult females captured during 1968–70.

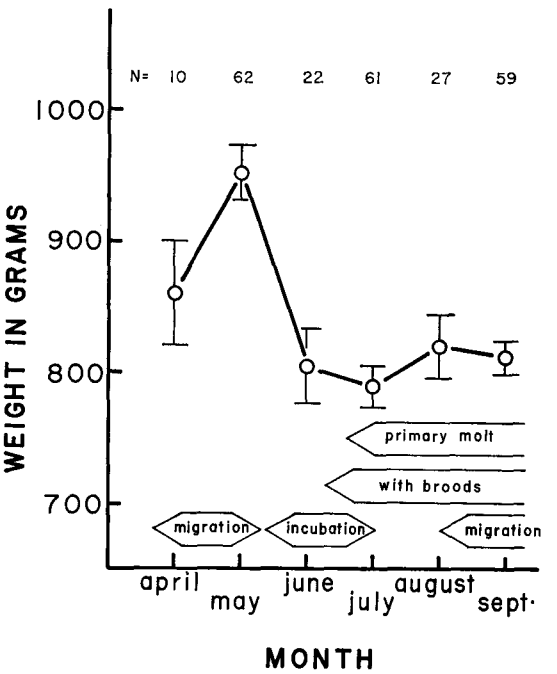

FIGURE 5. Average weight (± 2 SE) of yearling females captured during 1968–70.

TABLE 7. Average monthly weight (g) of adult female Blue Grouse, 1968–71.

	1968			1969			1970			1971		
	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$
April	–	–	–	6	913	33	6	1003	24	3	885	7
May	2	1050	–	20	1039	18	4	1132	60	3	995	29
June	5	890	30	6	773	25	13	841	16	13	812	5
July	39	863	8	20	829	10	5	848	13	6	809	5
Aug.	15	887	19	9	819	25	7	837	14	–	–	–
Sept.	26	842	11	30	836	9	41	858	10	35	872	10

TABLE 8. Average monthly weight (g) of yearling female Blue Grouse, 1968–71.

	1968			1969			1970			1971		
	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$	N	$\bar{X}$	$S_{\bar{x}}$
April	–	–	–	7	859	27	3	860	32	15	853	4
May	9	1002	21	29	950	17	24	937	15	44	940	2
June	6	858	21	9	792	21	7	774	21	22	821	6
July	11	800	16	24	820	11	26	759	12	35	783	3
Aug.	13	838	20	7	831	18	7	783	13	4	812	15
Sept.	23	827	9	14	821	14	22	795	11	35	827	10

in April were heavier than adults captured the previous September (fig. 3).

Summarizing, adult and yearling male Blue Grouse did not have significant changes in weight in spring or summer, but both adult and yearling females did. Maximum weights of females were reached in May and minimum weights, in June–September. In midsummer, hens with broods were lighter than hens without broods. Both adult males and females were heavier than their yearling counterparts, and it appears likely that yearlings gain weight over their second winter of life.

VARIATION BETWEEN YEARS

Since weight of adult and yearling males did not change throughout spring and summer, year-to-year comparisons were made by combining data of each age-class in each year. Yearly comparisons for females were made by combining data for brood hens only of each age-class in each year.

Table 10 presents data on average weight of grouse for all sex and age-classes in each year. One-way analysis of variance on these data showed significant variations in weight of all sex and age-classes. The largest absolute variation in average weight was in adult males which were nearly 90 g heavier in 1968 and 1970 than in 1969 and 1971. The general trends in weight between years can be summarized as follows:

	1968	1969	1970	1971
Adult Males	High	Low	High	Low
Yearling Males	High	Low	Low	High
Adult Females	High	Low	Intermediate	Low
Yearling Females	High	High	Low	Intermediate

TABLE 9. Weight (g) of hens captured with broods in June and July as compared to those captured without broods. Brood hens are lighter than lone hens.

	1968			1969			1970			1971		
	N	$\bar{X} \pm Se$		N	$\bar{X} \pm Se$		N	$\bar{X} \pm Se$		N	$\bar{X} \pm Se$	
Adults												
Brood Hens	44	866 ± 8	[c]	26	816 ± 11	[c]	18	842 ± 12	+	19	811 ± 7	+
Lone Hens	8	953 ± 23		4	935 ± 22		1	950		2	905	
Yearlings												
Brood Hens	17	820 ± 14	[b]	33	813 ± 10	[a]	33	762 ± 10	+	52	783 ± 8	[c]
Lone Hens	17	885 ± 15		10	847 ± 20		2	745		9	898 ± 29	

+ = no comparisons made, samples too small.
[a] $P \leq 0.1$
[b] $P \leq 0.01$
[c] $P \leq 0.001$

TABLE 10. Average weight (g) of Blue Grouse, 1968–71. Data for females are for brood females only.

		1968	1969	1970	1971	*F*	*P*
Adult Males	N	31	32	24	29	11.1	<0.001
	$\bar{X}$	1331	1240	1320	1237		
Yearling Males	N	11	35	19	64	4.1	<0.01
	$\bar{X}$	1130	1095	1071	1130		
Adult Females	N	43	29	22	19	5.9	<0.001
	$\bar{X}$	867	823	842	813		
Yearling Females	N	23	30	39	60	7.4	<0.001
	$\bar{X}$	825	817	765	788		

F is the results of analysis of variance; *P* is the probability of *F* arising by chance.

Weight of adult males and females tended to be highest in 1968 and 1970 and lowest in 1969 and 1971. Weight of yearling males was highest in 1968 and 1971 and lowest in the intervening years. Weight of yearling females was high in 1968 and 1969 and lower thereafter.

This inconsistent pattern of changes in weight in different sex and age-classes between years contrasts with the pattern demonstrated by Koskimies (1958) for Blackgame and Capercaillie. He attributed the variations in weight between years to weather, but as will be discussed, this seems unlikely in Blue Grouse.

DISCUSSION

Bendell (1955) studied grouse near Campbell River, Vancouver Island, but his data on weight are for birds without crops. This makes it difficult to make direct comparisons. Thus, weights he reports may be of little value in these comparisons. Boag (1965) gives average weights only, and while we can compare averages, without the variation in the averages we can make no statistical tests. Thus, his data are also of limited value for comparative purposes. Zwickel et al. (1966) recorded weights of grouse shot by hunters in Washington state in late autumn and their data are potentially useful for comparative purposes if no changes in weight occur in late autumn.

Zwickel et al. (1966) report an average weight for adult males of 1194 g and for adult females of 899 g. These weights are less for adult males and greater for adult females than the weights presented in this paper. Thus, adult males may be smaller and adult females larger in interior Blue Grouse than in the coastal races. This can be interpreted to mean that sexual dimorphism is more marked in the coast race than in the interior, but more evidence is needed to check this.

Seasonal variations in weight can potentially be attributed to several factors. Weight of male Blue Grouse does not change significantly from April–September. This is a time when male grouse are (a) defending a territory (adults and a small percentage of yearlings); (b) competing for mates; (c) changing diet from conifer needles to leaves and fruits (King 1968); and (d) initiating a complete body molt. These appear to be marked ecological and physiological changes but these changes do not cause a loss of weight. This suggests that energy for male grouse in summer is not limiting.

Unlike males, females have significant fluctuations in weight throughout summer. The major change in body weight of females appears closely related to egg-laying and incubation. To clarify this relationship, weights of females were reanalyzed in relationship to nesting history rather than date of capture. It is possible to determine the nesting history of a female if the date of hatch of her eggs is known. The date of hatch of her eggs can be determined if young from her brood are captured (Zwickel and Lance 1966). This analysis reduces sample sizes, since young from all broods were not captured and since many hens never had a brood.

As an illustration, suppose a female was captured on 15 May and weighed 925 g. Suppose she was relocated with 10-day-old chicks on 5 July. Then the chicks hatched on 25 June, which means the female probably started incubation on 31 May (26-day incubation period). Thus, the female was originally captured 16 days before start of incubation. In this way, weights in relation to nesting history can be compiled.

This analysis is summarized in figure 6. It clearly shows that weight of females changes in relation to nesting history. Weight is at a maximum 30–40 days prior to hatching and declines to a low level at, or shortly after, the time chicks hatch.

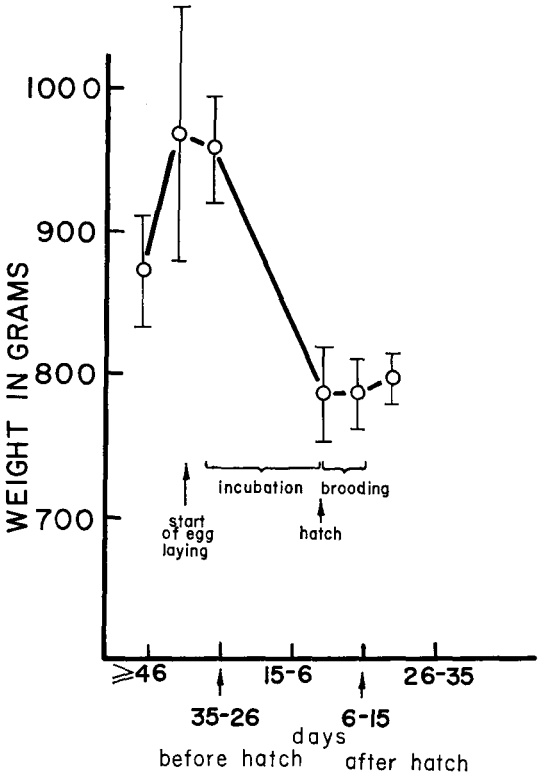

FIGURE 6. Average weight (± 2 SE) of yearling females (for 1971) in relation to nesting. Averages were calculated for 5-day periods before and after hatching of eggs by considering data for females with known nesting histories only, as explained in text.

Bendell (1955) concluded that weight of adult and yearling females did not change significantly throughout summer at Campbell River even though females in spring were heavy with eggs. Boag (1965) concluded that adult females in the Rocky Mountains of Alberta had a significant decline in weight in May and that yearling females did not have the same pattern of change as adults. The conclusions of both these authors contrast with those of this paper. Perhaps Bendell's conclusions were due to small sample sizes, especially in spring. In Boag's study, yearling females did not breed (as reported in Zwickel and Bendell 1967), while in this study they did breed. Since fluctuations in weight of females is closely related to breeding, this may be the reason for the difference.

The initial increase in weight of females in April often occurs at a time when new growth of plants has not begun. During egg-laying and incubation, females lose 20–25% of their body weight. A similar decline in weight of Ring-necked Pheasants (*Phasianus colchicus*) is caused by loss in weight of the reproductive tract, intestine, gizzard, spleen, pancreas, liver, and kidney (Breitenbach and Meyer 1959).

After chicks hatch, females begin a general molt. However, this molt appears to have little or no detrimental effect on weight of females. Female Blue Grouse are heavier in spring, prior to egg formation, than in autumn. This may be related to a seasonal deposition of fat known to occur in other birds (Breitenbach et al. 1963; King and Farner 1965; Hanson 1962) which is related to migration and hormonal levels. Whether this increase in weight occurs in late autumn, winter, or early spring is not known, but it seems unlikely that all of the increase occurs after arrival on the breeding range in early spring.

Stability of weight of male Blue Grouse during the breeding season contrasts with that for some other galliforms, such as California Quail (*Lophortyx californicus*), which lose weight throughout the breeding season (Lewin 1963). Perhaps the difference is related to the social structure of various species. For example, California Quail are monogamous and males help rear young. Blue Grouse are polygamous and males do not assist the females with broods.

The average weight of Blue Grouse measured in this study has varied from year to year. No adequate explanation for this variation seems obvious. Presumably, fluctuations in weight result to some extent from fluctuations in the environment. The most obvious environmental variables which may affect weight are nutrition, weather, and population density. However, any adequate explanation of these variations must explain why all segments of the population were not affected similarly.

Weather affects the weight of pheasants (Gates and Woehler 1968), Capercaillie, and Blackgame (Koskimies 1958). During my study, two winters were particularly severe (1968–69 and 1970–71). In 1968–69, the Canadian west coast had one of the most severe winters on record. Deep snow lasted well into April on my study areas. Again, 1970–71 was a severe winter and in April deep snow was still on portions of the study area. However, adults and yearlings did not follow the same pattern of weight change in these years. Adults, both males and females, were heaviest following mild winters. But weight of yearlings did not fluctuate in the same manner. Thus, if winter weather is to be implicated as affecting grouse weights, one must explain why age-classes were not always af-

TABLE 11. Breeding success of female Blue Grouse.

Age		1968	1969	1970	1971
Adults	$\bar{x}$ brood size	3.5	3.7	4.8	4.7
	% with broods	50.0	49.0	56.0	75.0
	Breeding success	1.75	1.81	2.69	3.51
Yearlings	$\bar{x}$ brood size	3.6	2.9	3.7	3.6
	% with broods	50.0	51.0	46.0	52.0
	Breeding success	1.80	1.48	1.70	1.87

Breeding success is defined as the average brood size times the percentage of females with chicks.

fected similarly and why yearling males and females had different patterns of variation.

Body weight of Red Grouse (*Lagopus lagopus scoticus*) in autumn is correlated with reproductive success the previous summer (Jenkins et al. 1963). I examined this aspect in Blue Grouse but found no correlation between breeding success and late summer weight (table 11; $r$adults = –0.612; $r$yearlings = –0.229).

A general hypothesis is that reproductive success of galliforms is governed by factors affecting the female prior to egg-laying (Jenkins et al. 1963; Southwood 1967; Zwickel and Bendell 1967). If true, weight is probably not an accurate measure of this condition, at least in Blue Grouse, since differences in breeding success between adults and yearlings (table 10) are more likely related to age rather than weight; and no correlation exists between weight and breeding success.

SUMMARY

Weight of adult and yearling male Blue Grouse is relatively stable in spring and summer and adults are heavier than yearlings. Significant seasonal fluctuations in weight of adult and yearling females are closely related to egg-laying, incubation, and raising of young. Adult females are heavier than yearlings. Molt does not appear to affect weight of any segment of the population. Weight of all sex- and age-classes varied significantly from year to year but no adequate explanation of the variations can be given. The patterns of variation were not consistent between age-classes or sexes. There were no correlations between breeding success and weight.

ACKNOWLEDGMENTS

This research was supported by the National Research Council of Canada (predoctoral scholarship), American Ornithologists' Union (Josselyn Van Tyne Memorial Grant), British Columbia Fish and Wildlife Branch and the University of Alberta (scholarship). This support is appreciated.

Thanks go to MacMillan-Bloedel Ltd., Sproat Lake Division, and their personnel, for extending permission to study grouse on their land. Bud Smith and Bill Hazeldine of the B.C. Fish and Wildlife Branch helped collect some of the data at checking stations in autumn; this help was invaluable. Several field assistants have also aided in collection of these data. Thanks are extended to all of these persons. F. C. Zwickel read versions of the manuscript and made several valuable suggestions.

LITERATURE CITED

BALDWIN, S. P., AND S. C. KENDEIGH. 1938. Variations in the weight of birds. Auk 55:416–467.

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

BENDELL, J. F., AND P. W. ELLIOTT. 1966. Habitat selection in Blue Grouse. Condor 68:431–446.

BENDELL, J. F., AND P. W. ELLIOTT. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildl. Serv. Rep. Ser. No. 4. 76 p.

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

BREITENBACH, R. P., AND R. K. MEYER. 1959. Effect of incubation and brooding on fat, visceral weights and body weight of hen pheasants (*Phasianus colchicus*). Poultry Sci. 38:1014–1026.

BREITENBACH, R. P., C. L. NAGRA, AND R. K. MEYER. 1963. Effect of limited food intake on cyclic annual changes in Ring-Necked pheasant hens. J. Wildl. Mgmt. 27:24–36.

GATES, J. M., AND E. WOEHLER. 1968. Winter weight loss related to subsequent weights and reproduction in penned pheasants. J. Wildl. Mgmt. 32:234–247.

HANSON, H. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. Arctic Inst. N. Amer. Tech. Paper No. 12, p. 1–68.

JENKINS, D., A. WATSON, AND G. R. MILLER. 1963. Population studies on Red Grouse, *Lagopus lagopus scoticus* (Lath.), in north-east Scotland. J. Anim. Ecol. 32:317–376.

KING, R. D. 1968. Food habits in relation to the ecology and population dynamics of Blue Grouse. M.Sc. thesis, Univ. of British Columbia. 62 p.

KING, J. R., AND D. S. FARNER. 1965. Studies of fat deposition in migratory birds. Ann. N.Y. Acad. Sci. 131:422–440.

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.

KRAJINA, V. J. 1969. Ecology of forest trees in British Columbia. Ecol. Western N. Amer. 2: 1–146.

LEWIN, V. 1963. Reproduction and development of young in a population of California Quail. Condor 65:249–278.

MAYR, E. 1963. Animal species and evolution. Belknap Press, Cambridge, Mass. 797 p.

OWEN, D. F. 1954. The winter weight of titmice. Ibis 96:299–309.

REDFIELD, J. A. 1972. Demography and genetics in colonizing populations of Blue Grouse (*Dendragapus obscurus*). Ph.D. thesis, Univ. of Alberta, 115 p.

REDFIELD, J. A., F. C. ZWICKEL, AND J. F. BENDELL. 1970. Effects of fire on numbers of Blue

Grouse. Ann. Tall Timbers Fire Ecol. Conf., Proc. 10:63–83.

RICHDALE, L. E. 1957. A population study of Penguins. Oxford Univ. Press, Oxford. 195 p.

SOUTHWOOD, T. R. E. 1967. The ecology of the partridge. II. The role of pre-hatching influences. J. Anim. Ecol. 36:557–562.

ZWICKEL, F. C., AND J. F. BENDELL. 1967. Early mortality and the regulation of numbers in Blue Grouse. Can. J. Zool. 45:817–851.

ZWICKEL, F. C., J. H. BRIGHAM, AND I. O. BUSS. 1966. Autumn weights of Blue Grouse in north-central Washington, 1954 to 1963. Condor 68: 488–496.

ZWICKEL, F. C., AND A. N. LANCE. 1966. Determining the age of young Blue Grouse. J. Wildl. Mgmt. 30:712–717.

Accepted for publication 11 August 1972.