SEASONAL CHANGES IN THE INTERNAL ANATOMY OF SPRUCE GROUSE IN ALBERTA

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A relationship exists between the level of fiber in the diet of gallinaceous birds and the gross anatomy of their gastrointestinal tracts. Leopold (1953) reported that species living largely on leafy materials (high fiber content) have relatively larger digestive systems than do those eating seeds and fruits (low fiber content); this relationship also exists intraspecifically when populations in different areas feed on different foods. More recently Lewin (1963) recorded that, even within a single population, the characteristics of the digestive system vary seasonally with changes in the fiber content of the diet.

Spruce Grouse (*Canachites canadensis*) eat foods of relatively low fiber content in summer, when fruit is an important item, but of very high fiber content during periods of extensive snow cover when they eat only conifer needles (Ellison, 1966; Pendergast and Boag, 1970). Hypothetically this change in diet should be correlated with structural changes in these birds' digestive systems. We investigated this hypothesis as it related to the gross anatomy of the digestive system as well as to other internal organs of this grouse.

METHODS

A sample of Spruce Grouse was shot each month of the year in the Swan Hills of central Alberta. Weights of the carcass, pectoral muscles, liver, heart, and pancreas were recorded in the field, as were linear measurements of the small and large intestine and the caeca. The crop, ventriculus, and large intestine with contents were quick-frozen on dry ice in the field. Subsequently these organs were thawed, emptied, and weighed. All organs weighed were first freed of excess fluids and adhering tissues, such as depot fat. The quantity of subcutaneous and mesenteric fat was estimated subjectively in all birds autopsied.

To compare the viscera of birds on the changing natural diet to those on a constant diet, two male grouse were held in captivity from August 1968 to February and April 1969 (Pendergast and Boag, 1971a) on a diet of mainly pelleted commercial turkey mash.

In comparing data between sexes or periods of time, all individuals were combined for any given month. This was felt justifiable because the chronology of events in the reproductive and postreproductive periods were relatively closely synchronized in this species (McCourt, 1969; McLachlin, 1970).

RESULTS AND DISCUSSION

Body weight has been used as an index of general condition in grouse (Bump et al., 1947), the assumption being that peak annual weight is associated with peak condition. We found body weight of Spruce Grouse

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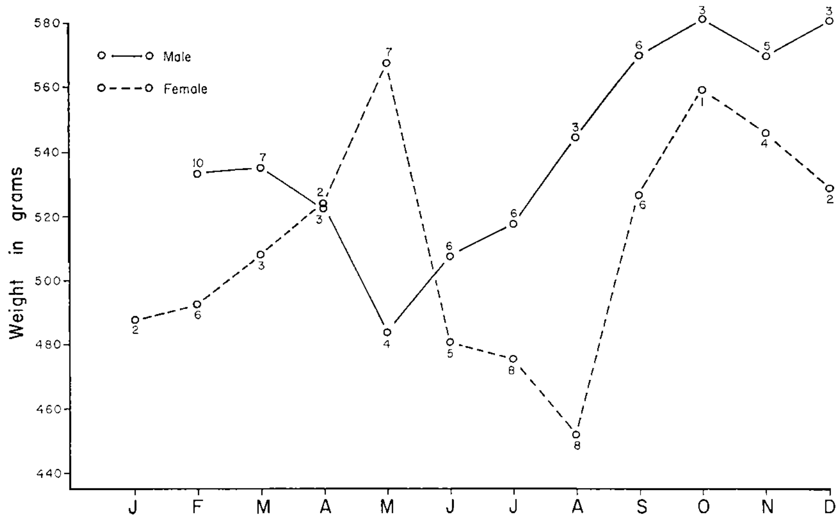

Figure 1. Mean body weight from monthly samples of adult Spruce Grouse shot in the Swan Hills, Alberta. Sample size adjacent to each mean value.

varied from season to season (Figure 1). Among males it reached maximal levels in early winter when birds were largely arboreal and their diet virtually monophagous (Pendergast and Boag, 1970); subsequently body weight declined to reach minimal levels in May at the peak of the breeding season (McCourt, 1969; McLachlin, 1970). The body weight of females followed a different seasonal pattern; maximal weights were achieved in May when breeding females were gravid and minimal weights in August after incubation and the postnuptial moult.

The greatest contrast in the diet of Spruce Grouse is between that of summer (June, July, August) when fruits of forest-floor plants are the major component, and winter (December, January, February) when they live essentially on conifer browse (Pendergast and Boag, 1970). Comparing weights during these two periods showed both sexes were heavier in winter than in summer (Table 1). Thus it appears that Spruce Grouse achieve maximum body condition during the winter when they are suspected of being largely arboreal and known to be virtually monophagous.

We examined the extent to which these seasonal changes in body weight were reflected in the skeletal musculature. We chose the M. pectoralis and M. supracoracoideus as indicators. Changes in the weight of these muscles (Figure 2) apparently followed a pattern similar to that of total body weight, but the difference between summer and winter weights was not significant (Table 1). Nevertheless the weight of both

TABLE 1
STATISTICAL COMPARISON OF ANATOMICAL PARAMETERS IN SPRUCE GROUSE

Comparison		Statistical test[1]	Probability
Weights (winter vs summer)			
Total	♂	White rank (n_1 = 13, n_2 = 15) = 155	< 0.10
	♀	White rank (n_1 = 10, n_2 = 21) = 112	< 0.05
M. pectoralis	♂	Pooled t (22 df) = 1.72	> 0.10
	♀	Pooled t (24 df) = 0.62	> 0.10
M. supracoracoideus	♂	Pooled t (22 df) = 0.10	> 0.10
	♀	Pooled t (24 df) = 0.10	> 0.10
Heart	♂	Pooled t (18 df) = 2.22	< 0.05
	♀	Pooled t (26 df) = 3.37	< 0.001
Crop	♂	Pooled t (19 df) = 4.11	< 0.001
	♀	Pooled t (25 df) = 3.47	< 0.01
Ventriculus	♂	Pooled t (20 df) = 10.17	< 0.001
	♀	Pooled t (26 df) = 8.10	< 0.001
Pancreas	♂	Pooled t (16 df) = 2.32	< 0.05
	♀	Pooled t (20 df) = 3.81	< 0.01
Liver	♂	Pooled t (20 df) = 2.00	< 0.10
	♀	Pooled t (26 df) = 1.36	> 0.10
Lengths (winter vs summer)			
Small intestine	♂	Pooled t (19 df) = 2.34	< 0.05
	♀	Pooled t (25 df) = 0.70	> 0.10
Large intestine	♂	Pooled t (17 df) = 5.13	< 0.001
	♀	Pooled t (27 df) = 3.36	< 0.01
Caecum	♂	Pooled t (21 df) = 6.05	< 0.001
	♀	Pooled t (26 df) = 6.86	< 0.001
Correlations (total weight (g) with)			
M. pectoralis (g)	♂	r (9 df) = 0.85	< 0.001
	♀	r (8 df) = 0.75	< 0.05
M. supracoracoideus (g)	♂	r (9 df) = 0.89	< 0.001
	♀	r (8 df) = 0.70	< 0.05
Heart	♂	r (9 df) = 0.58	< 0.10
	♀	r (10 df) = 0.70	< 0.05
Crop (g)	♂	r (9 df) = 0.56	< 0.10
	♀	r (10 df) = 0.73	< 0.01
Ventriculus (g)	♂	r (9 df) = 0.39	> 0.01
	♀	r (10 df) = 0.58	< 0.10
Pancreas (g)	♂	r (9 df) = 0.56	< 0.05
	♀	r (9 df) = 0.56	< 0.10
Liver (g)	♂	r (9 df) = 0.37	> 0.10
	♀	r (10 df) = −0.97	< 0.10
Small intestine (mm)	♂	r (9 df) = 0.51	> 0.001
	♀	r (10 df) = 0.27	> 0.10
Large intestine (mm)	♂	r (9 df) = 0.19	> 0.10
	♀	r (10 df) = 0.33	> 0.10
Caecum (mm)	♂	r (9 df) = 0.07	> 0.10
	♀	r (10 df) = 0.42	> 0.10

[1] White rank test from Bradley (1968), pooled t test from Steel and Torrie (1960).

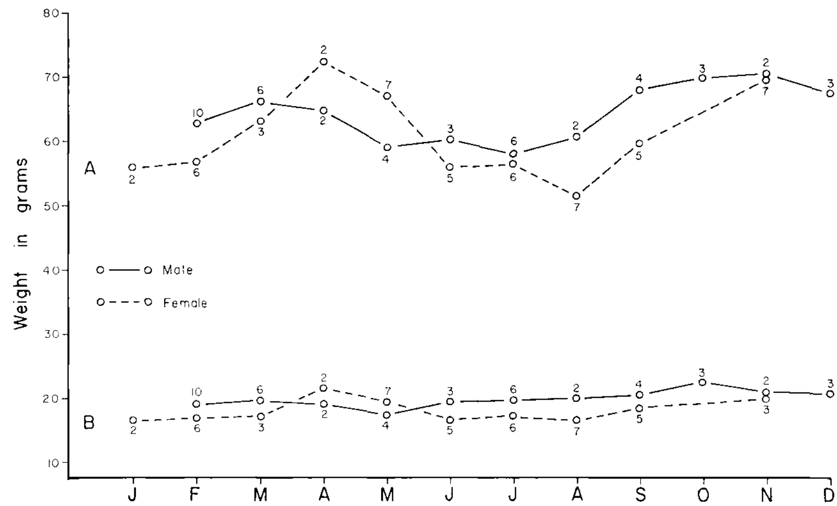

Figure 2. Mean weights of the pectoral muscles from monthly samples of adult Spruce Grouse. Sample size adjacent to each mean value. A, M. pectoralis; B, M. supracoracoideus.

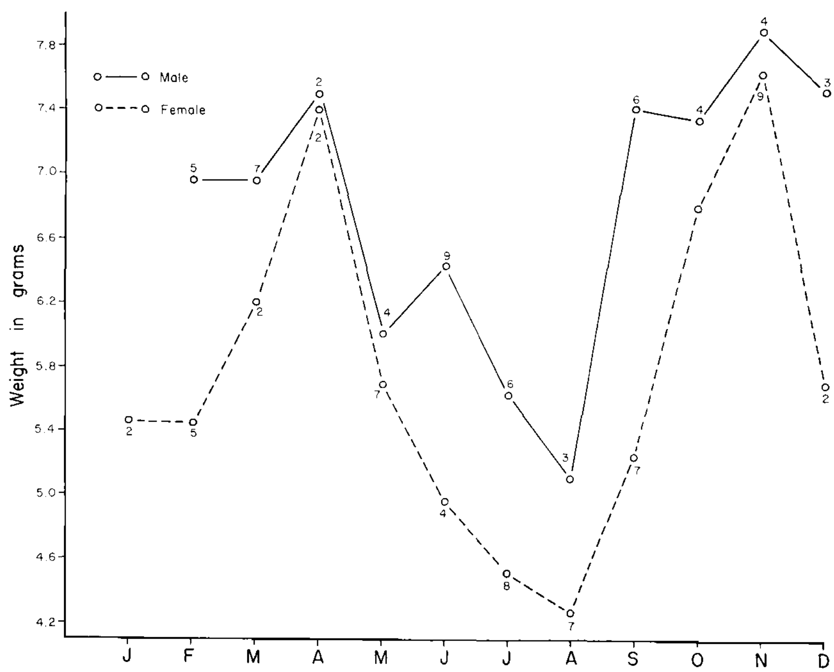

Figure 3. Mean weights of the heart from monthly samples of adult Spruce Grouse. Sample size adjacent to each mean value.

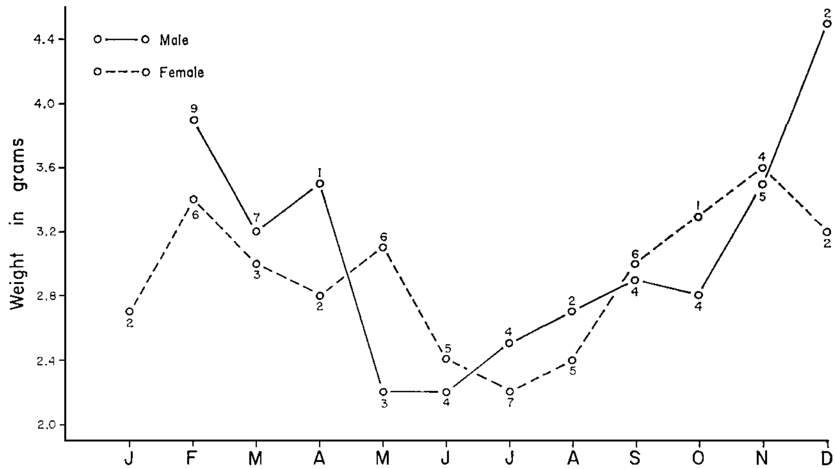

Figure 4. Mean weights of the empty crop from monthly samples of adult Spruce Grouse. Sample size adjacent to each mean value.

muscles was significantly correlated with total body weight (Table 1). The average contribution made by these two muscles to the monthly change in body weight was 17 percent, which indicates that the sketetal musculature makes a major contribution to changes in the total weight. This change may reflect intramuscular deposition of fat as suggested by Braun (1971).

The weight of the heart (Figure 3), like that of skeletal muscle, followed a pattern of seasonal change similar to body weight. Mean winter weights exceeded summer weights for both sexes (Table 1). Such changes in the weight characteristics of the heart suggest a response either to the same factors causing a presumed passive change in skeletal musculature, or to factors associated with a need for changes in blood flow, such as increased stroke-volume or heart rate, either of which would actively exercise the heart and cause changes in its mass.

Seasonal changes in the digestive system and its derivatives were reflected in both their weights and lengths. Weights of empty crops (Figure 4) from each sex were significantly greater for the samples taken in winter than for those taken in summer (Table 1). The weight dynamics for this organ follow closely those of body weight. Likewise, weights of empty ventriculi (Figure 5) were significantly heavier from birds shot in winter than from those shot in summer for both sexes (Table 1). Changes in the weight of these two organs were probably in response to the more fibrous and resistant winter diet of conifer needles. An increased thickness of the linings of these organs in response to the

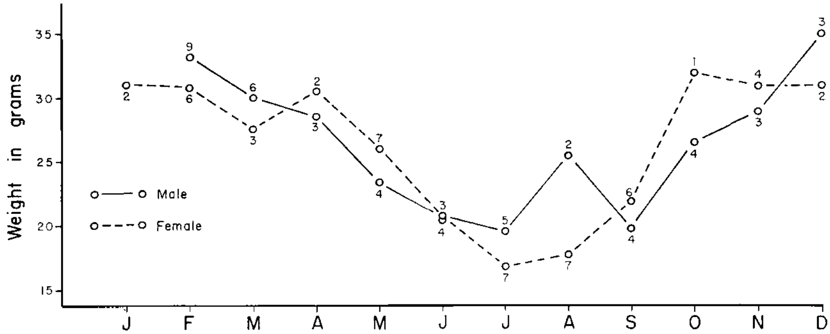

Figure 5. Mean weights of the empty ventriculus from monthly samples of adult Spruce Grouse. Sample size adjacent to each mean value.

harsher physical nature of the food and an active exercising of the musculature in response to the tougher foods would result in an increased mass.

Two organs derived from and intimately connected with the digestive system are the pancreas and liver. The former (Figure 6A) shows seasonal changes similar to those of the crop and ventriculus. Among both sexes the winter weight of the pancreas significantly exceeded that of the summer weight and seasonal changes followed those of body weight

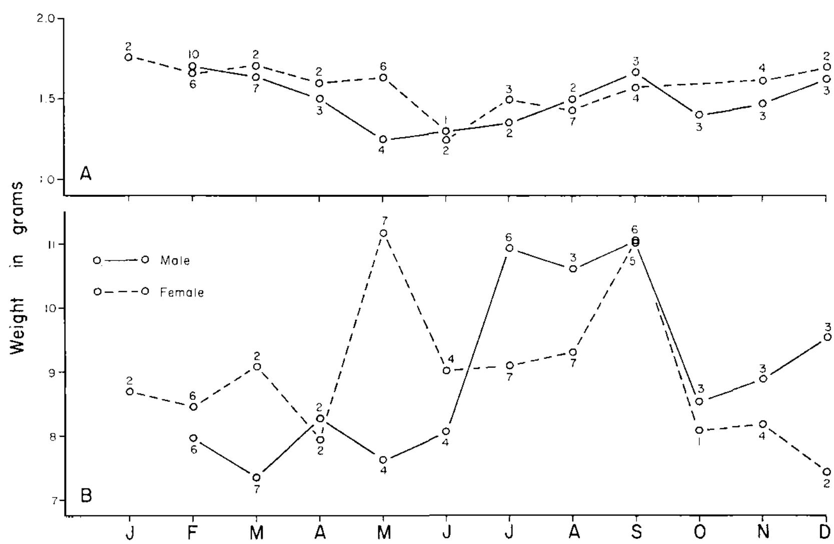

Figure 6. Mean weights of the pancreas and liver from monthly samples of adult Spruce Grouse. Sample size adjacent to each mean value. A, pancreas; B, liver.

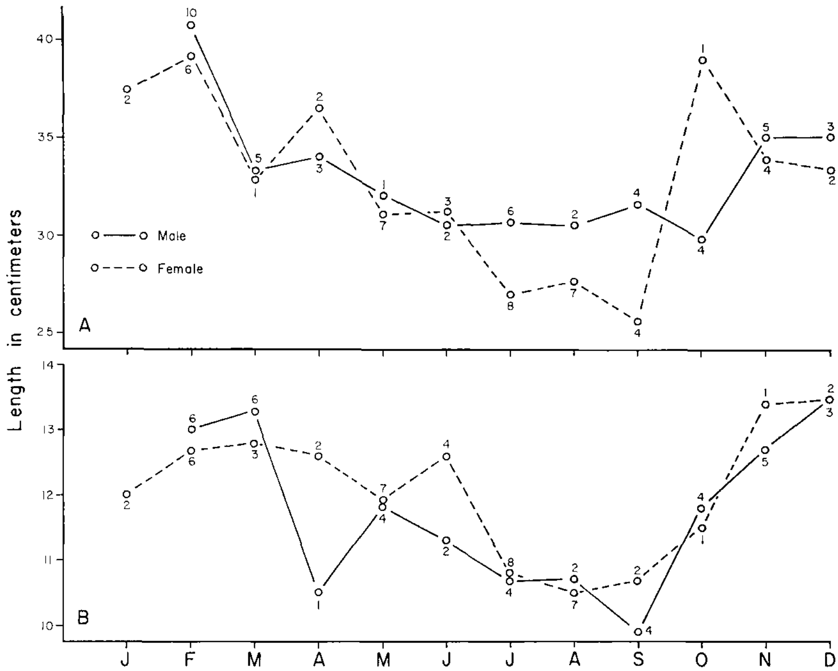

Figure 7. Mean lengths of the caecum and large intestine from monthly samples of adult Spruce Grouse. Sample size adjacent to each mean value. A, caecum; B, large intestine.

(Table 1). The pattern of weight change in the liver did not resemble that of any other organ weighed (Figure 6B). Weights of livers taken from both sexes of Spruce Grouse collected during the winter were less than those taken from birds shot in the summer; but the differences were not significant (Table 1). The pattern of change in liver weight was the converse of that in body weight among females but showed no correlation with body weight among males (Table 1). Changes in weight of the liver undoubtedly reflect the birds' changing physiological condition, probably in response to dietary changes (Magnan, 1913), which could affect such phenomena as lipid and glycogen storage.

Lengths of the small intestine did not appear to change with the same rhythmicity throughout the year as did the lengths of the caeca (Figure 7A) and large intestine (Figure 7B). Nevertheless among male Spruce Grouse the small intestine from winter-shot birds was significantly longer than those from summer-shot birds; such was not the case among females (Table 1), nor was there any correlation between the lengths of the small intestine and body weight. This was in contrast to

TABLE 2
ANATOMICAL CHARACTERISTICS OF SPRUCE GROUSE HELD FOR VARYING PERIODS IN CAPTIVITY COMPARED WITH THOSE OF WILD BIRDS KILLED AT SIMILAR TIMES OF THE YEAR

	Values for captive birds		Mean values for comparable wild birds	
	A	B	A	B
Age and sex	Adult ♂	Adult ♂	Adult ♂	Adult ♂
Time in captivity (days)	112	281	0	0
Date killed	24 Feb.	16 Apr.	Feb.	Apr.
Total weight (g)	617.0	—	533.2	521.5
M. pectoralis (g)	80.3	67.9	62.5	63.0
M. supracoracoideus (g)	27.8	21.8	19.0	18.1
Heart (g)	8.9	9.4	6.9	7.6
Pancreas (g)	1.8	—	1.7	1.5
Liver (g)	19.4	23.0	8.0	8.3
Empty ventriculus (g)	20.8	18.5	33.0	29.5
Empty crop (g)	—	2.2	3.9	3.6
Small intestine (mm)	—	700	900	710
Large intestine (mm)	92	90	130	105
Caecum (mm)	270	170	410	340

the significantly greater length of the large intestine and of the caeca from winter-shot grouse (Table 1). The lengths of these organs were not correlated with total body weight (Table 1). Changes in the length of the small intestine did not follow those of other organs. This may reflect differential stretching of the intestine while measuring it. The nature and extent of its contents seemed to influence the degree to which this relatively elongate and thin-walled organ could be stretched. On the other hand if there was change in the absorptive surface of the small intestines, it may have been only a function of changes in the length of the mucosal villi as found in California Quail (*Lophortyx californicus*) (Lewin, 1963) rather than overall organ length.

Changes in the weight-length characteristics of the gastrointestinal tracts appear to be mainly the result of changes in the diet. Spruce Grouse held in captivity (Pendergast and Boag, 1971a) on a diet composed largely of commercial poultry pellets failed to show the increases in weights and lengths of components of the gastrointestinal tract during winter demonstrated by members of the same population in the wild (Table 2).

In summary the body weight of Spruce Grouse is greater in winter than in summer. Although the winter diet produces a significant increase in the mass of the gastrointestinal tract, this was insufficient to explain total differences in body weight between summer- and winter-shot specimens. The total weight change required the combined increases in weight of a number of anatomical structures including the musculature, gastrointestinal tract, and associated organs. Added to these was the increased mass of the reproductive system in females, which explained the peak body weight in May in this sex. Deposition of depots of body fat, located largely in the mesenteries, was not considered a significant factor in weight changes of Spruce Grouse. In males the amount of depot fat was always very small and remained relatively constant throughout the year. In females depot body fat increased slightly prior to laying but, as in males, it remained small and relatively constant at other times.

The annual cycle in body weight of Spruce Grouse is remarkably similar to that found in other gallinaceous birds, for example California Quail (Lewin, 1963, Figure 12), and Blue Grouse (*Dendragapus obscurus*) (Boag, 1958, Figure 4). This suggests a common pattern of weight change in this order of birds, which also tend to show a general changeover in diet between winter and summer.

Lewin (1963) stated that among California Quail the increase in body weight prior to oviposition could be explained by the increase in weight of the reproductive system. In Spruce Grouse the increase in weight of the reproductive tract is not responsible alone for the increase in weight of the gravid female; the body muscles and gastrointestinal tract also make significant contributions. This is similar to the situation Kirkpatric (1944) described in female pheasants (*Phasianus colchichus*).

The nature of the diet appears to affect markedly the gross anatomy of the gastrointestinal tract. A diet low in fiber content, fed captive Spruce Grouse, failed to produce an increase in mass of the gastrointestinal tract comparable to that occurring in the population feeding on a diet of high fiber content. Thus the anatomical changes recorded are apparently stimulated by the nature of the food and not by the same factors affecting the reproductive tract. It remains to be determined whether the stimulus is physical or chemical or both. The effect of continued consumption of some conifer needles into the summer season appears to be the explanation for a gastrointestinal tract of winter dimensions in an August-shot male—the crop and gut contents of this bird were largely conifer needles. This is reflected in Figure 5 where the weight of this bird's ventriculus was sufficient to raise the mean weight for this organ from August-shot birds well above that of both July and September.

The increased biomass of the gastrointestinal tract in winter would increase the power of the musculature particularly of the ventriculus, expand the surface area available for absorption in the intestine and caecum, and augment the capacity of the tract to harbor a resident microbial fauna (particularly the caeca). All these factors are probably important in enabling the grouse to cope with the large volume of extremely fibrous foods consumed in winter. The increased biomass of the body in winter would be of advantage to the grouse in thermoregulation.

It is noteworthy that Spruce Grouse achieved maximum condition on a diet of conifer browse alone, and that during the 2 years of this study, females came into breeding condition on a diet of conifer needles and small amounts of over-wintered berries of *Vaccinium vitis-idaea* (Pendergast and Boag, 1970). This suggests that the winter diet is more than adequate for the maintenance of body condition (Pendergast and Boag, 1971b). The fact that female Spruce Grouse do not appear to take any new plant growth prior to laying raises the question of egg production and egg quality under such circumstances. Moss et al. (1971) have shown that captive Red Grouse (*Lagopus lagopus scoticus*), given a supplement of heather (*Calluna vulgaris*) that was beginning to grow in the spring, laid more eggs and at a faster rate than birds given a supplement of dormant winter heather. Earlier, Jenkins et al. (1965) showed that chick survival in Red Grouse was determined by egg quality and Moss (1967) has suggested that the quality (protein and phosphorus content) of the spring diet of the female is important in governing egg quality. These hypotheses need to be tested in Spruce Grouse.

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SUMMARY

Changes in the internal anatomy of Spruce Grouse were recorded from adult specimens shot each month of the year in the Swan Hills of Alberta. Total body weight in both sexes was greater in winter than in summer, maximal weights in males being achieved in December, and in females in May. Changes in the weight of both skeletal and cardiac muscle followed closely changes in body weight, being significantly heavier in winter- than in summer-shot specimens. Likewise changes in the weight of the empty crop, ventriculus, and pancreas were positively correlated with body weight, but the liver differed in being heavier in summer than in winter. In addition to changes in weight, the lengths of the small and large intestine and caeca varied seasonally, being longer from winter- than from summer-shot specimens. Changes in the weight and length characteristics of the gastrointestinal tract were correlated with changes in the diet. Fat deposition was not a significant factor in weight changes in this grouse.

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