NUTRITIONAL ASPECTS OF THE DIET OF SPRUCE GROUSE IN CENTRAL ALBERTA

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Spruce Grouse (*Canachites canadensis*) rely heavily on conifer needles as a dietary item (Ellison 1966; Pendergast and Boag 1970). In central Alberta this food constitutes 79 per cent of the annual diet on a dry weight basis. During that part of the year when the ground is snow-covered this percentage rises to 99 (Pendergast and Boag 1970). Such heavy reliance on a particular food suggests that it is nutritionally adequate. However, when compared with commercially prepared poultry rations, conifer browse is low in nutrients, particularly protein (Beaton et al. 1965; Ellison 1966; Boag and Kiceniuk 1968). But since Spruce Grouse do survive on a diet of conifer browse, the question is raised as to how they extract sufficient nutrients from it to survive.

This paper reports on the level of some nutrients in the major items of the annual diet of Spruce Grouse from central Alberta, and on the digestion of the main food of this population, needles of lodgepole pine (*Pinus contorta*).

METHODS

A sample of Spruce Grouse was shot each month in the Swan Hills of central Alberta. Foods consumed by these grouse were removed from their crops, sorted into species components, and freeze dried (Pendergast and Boag 1970). Where necessary, foods of similar type from different crops were combined to give samples of 10 g dry weight for analyses of nutrient content and gross energy levels. Additional samples of some items were collected by hand in the field to compare with those selected by the grouse.

Samples of the major food items were analyzed by the Alberta Soil and Feed Testing Laboratory for the following constituents: residual moisture, lignin, crude fiber, protein, calcium, phosphorus, magnesium, potassium, and sodium. Caloric values for the same foods were measured with a Parr oxygen-bomb calorimeter.

The amino-acid content of the needles of lodgepole pine was determined by the Department of Biochemistry, University of Alberta. The eight samples analyzed were prepared according to a procedure outlined by Moore and Stein (1963).

The availability of nutrients in pine needles was determined through feeding experiments carried out in January under below-freezing conditions out of doors. Two groups of Spruce Grouse, each with a different dietary history, were housed individually in cages measuring 51 × 102 × 51 cm. Daily they were given an excess of preweighed fresh pine boughs and snow. The weight of the needles ingested daily was determined by reweighing the browsed boughs and any needles which were dropped. Caecal and intestinal droppings were sorted while frozen and analyzed by the same procedure used in analyzing foods.

RESULTS

ANALYSES OF FOOD

Energy content. The gross energy values for the major foods of spruce grouse in central Alberta are presented in table 1. Of the foods tested, the gross energy values were greatest for mature conifer needles, the major item in the diet. These caloric values agree closely with those recorded for conifers elsewhere (Ellison 1966; Boag and Kiceniuk 1968). It is noteworthy, however, that combined with the high values of gross energy were also high levels of crude fiber and lignin, suggesting that much of the energy present in the food may not have been available to the grouse. This situation is changed somewhat when the diet is composed of other foods in addition to conifer browse, for example, when large amounts of *Vaccinium* spp. are taken in summer and autumn (Pendergast and Boag 1970). These latter species, although they have lower gross energy values, also have lower levels of crude fiber and lignin (table 1). The gross energy level recorded in nearly all major foods was greater than that present in the commercial poultry rations used (4.68 Kcal/g). However, the availability of this energy would depend on the ability of grouse to extract it on a unit of time basis. This can only be determined through digestibility studies.

TABLE 1. Levels of chemical constituents and gross energy values of foods utilized by Spruce Grouse in the Swan Hills, Alberta.[a]

Foods	Sample size	Gross energy (Kcal/g)	% of dry weight							
			Lignin	Crude fiber	Protein[b]	Ca	P	Mg	K	Na
Musci spp. spore capsules	1	4.33	12	28	8.8	.08	.08	.03	.40	.06
Equisetum spp. stems and tips	1	4.26	–	–	17.6	–	–	–	–	–
Pinus contorta needles	16	5.32	26	42	8.2	.14	.12	.11	.52	.22
Picea spp.										
needles	2	5.19	16	31	5.8	.43	.10	.07	.39	.12
needle buds	2	4.89	22	30	16.8	.08	.15	.04	.55	.07
Carex spp. fruit	1	5.15	–	–	15.0	–	–	–	–	–
Streptopus amplexifolius green fruit	1	–	–	–	19.0	–	–	–	–	–
Vaccinium membranaceum										
leaves	2	4.97	13	23	14.3	.18	.10	.11	.64	.06
flowers	1	5.10	–	–	18.3	–	–	–	–	–
green fruit	1	5.07	–	–	11.7	–	–	–	–	–
ripe fruit	1	4.95	23	38	10.1	.15	.24	.10	1.03	.41
Vaccinium vitis-idaea										
new fruit	1	4.70	12	20	3.8	.04	.05	.02	.27	.05
over-wintered fruit	1	4.91	22	35	5.1	.10	.14	.08	.11	.21

[a] Mean values given for sample sizes >1; forest floor species collected in spring and summer, conifer needles in winter and spring.
[b] Nitrogen × 6.25.

Protein content. The level of protein in conifer needles was less than 9 per cent (table 1). This value is low by standards used in commercial poultry diets (National Research Council 1966). On the other hand, the levels of protein in the forest floor species, with the exception of *V. vitis-idaea*, were adequate by the same standard. Assuming that grouse require nutrients in the same proportions as do poultry, low levels of protein in the diet could be compensated for by processing greater volumes of food. Such a situation is suggested in the greater crop volumes recorded for grouse killed in the winter when the diet was entirely of conifer needles (Pendergast and Boag 1970).

The mean level of protein recorded for the needles of lodgepole pine (8.2 per cent of dry weight) was higher than that reported for this species in other areas (Beaton et al. 1965, (7.5 per cent; Boag and Kiceniuk 1968, 4.5 per cent).

Mineral content. The levels of calcium and phosphorus in all foods analyzed were low (table 1) when compared with the requirements of domestic fowl as given by the Natural Research Council (1966) (calcium, 2.25 and 1.0 per cent, and phosphorus, 0.6 and 0.6 per cent for laying hens and growing chicks, respectively). However, these "required" levels do exceed critical levels for poultry. Furthermore, the requirements for laying fowl undoubtedly exceed those of laying Spruce Grouse as the latter produce fewer eggs (only 4–7, Godfrey 1966) and at a slower rate (approximately one egg every second day, McCourt 1969; Pendergast and Boag 1971).

The mineral constituents in pine needles were similar to those found by Beaton et al. (1965). The only significant difference between pine and spruce in mineral content was in the level of calcium; spruce needles contained three times as much as pine (table 1). The consumption of spruce needles by female Spruce Grouse increased during May and June at the onset of egg production (table 2), suggesting a possible selection of a food high in calicum.

TABLE 2. Amounts of spruce and pine needles in the diet of Spruce Grouse during the spring months in central Alberta (mean per cent of dry weight).

Sex	*n*	% spruce	% pine
March–April			
♂	8	26.2	50.5
♀	5	0.0	99.0
May–June			
♂	8	21.2	49.6
♀	12	47.4	26.9

TABLE 3. Amounts of pine needles eaten and droppings produced by six captive Spruce Grouse held in individual outdoor cages during January 1968 at Edmonton, Alberta (results based on a total of 51 grouse days).

	Dry weight (g/bird per day)	
	$\bar{x}$	SD
Needles eaten	40.4	13.7
Caecal droppings produced	2.2	1.0
Intestinal droppings produced	27.3	8.2
Total droppings produced	29.5	
Difference between total food and droppings	10.9	

The nutrient content of foods has little meaning without knowing the availability of these nutrients, through digestion, to the grouse. This information can only be obtained through feeding experiments.

DIGESTION OF PINE NEEDLES BY SPRUCE GROUSE

Energy. Available energy or metabolizable energy (ME) is equal to the difference between total calories present in the food and droppings measured over a unit of time. It is usual to express ME in kilocalories per gram of food consumed. The data necessary for these calculations were obtained through feeding experiments using pine needles as the only food (tables 3 and 4).

Based on dry weight alone approximately 25 per cent of pine needles eaten are absorbed. However to determine the actual energy assimilated, it is also necessary to consider the caloric value of the food and droppings. Maynard and Loosli (1962) have based calculations of ME on the total dry weight of food eaten and droppings produced over a unit of time. ME $= [(ac - bd)/c]$ Kcal/g of food where: a = energy per gram of food; b = energy per gram of droppings; c = dry weight of food consumed per unit of time; and d = dry weight of droppings produced per unit of time.

Using the results of the feeding experiments (table 3) and the determinations of caloric values for food and droppings (table 4), the ME of lodgepole pine needles was calculated to be 1.56 Kcal/g. This is equal to 29.8 per cent of the gross energy in pine needles.

Thus the ability of Spruce Grouse to digest and assimilate organic nutrients from pine needles, under the conditions stated, would appear to be low. However, the apparent digestibility of this food (29.8 per cent) corresponds closely to 31 per cent reported for the stems of blueberry (*Vaccinium myrtillus*) digested by Willow Ptarmigan (*Lagopus lagopus*) (Pullianinen et al. 1968), and 21–30 per cent for the shoots of heather (*Calluna vulgaris*) digested by Red Grouse (*Lagopus l. scoticus*) in Scotland (Moss and Parkinson 1971). The variation in the ability of Red Grouse to digest heather is related to their ability to break down and assimilate the components of lignin and cellulose (Moss and Parkinson 1971). We investigated the digestion of lignin by captive Spruce Grouse by using it as the marker in a formula presented by Forbes and Garrigus (1948) for the calculation of ME:

$$ME = [1 - (e/f)(b/a)]a \text{ Kcal/g of food,}$$

where: a = energy per gram of food; b = energy per gram of droppings; e = per cent lignin in food; and f = per cent lignin in droppings.

Based on data presented in tables 3 and 4, the ME in lodgepole pine needles was calculated to be 1.53 Kcal/g. This is equal to 29.2 per cent of the gross energy in pine needles.

If lignin had been digested, the proportion in the droppings would have been less than recorded and the ME value would have differed from that previously calculated. However, since the two ME values agree closely we have concluded that lingnin was not digested. Moss and Parkinson (1971) believe that the extent to which lignin is digested is

TABLE 4. Levels of gross energy, protein, crude fiber, and lignin in food and feces of six captive Spruce Grouse held in individual outdoor cages in January 1968 at Edmonton, Alberta, and fed only lodgepole pine needles.

		Gross energy (Kcal/g)		Protein (% dry wt.)		Crude fiber (% dry wt.)		Lignin (% dry wt.)	
Item analyzed	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Pine needles	5	5.24	0.03	8.36	1.52	39.62	1.72	21.05	2.07
Caecal feces	9	5.58	0.04	20.84	2.36	19.48	6.12	13.74	5.91
Intestinal feces	11	5.00	0.10	14.33	1.05	53.02	4.78	29.78	3.33
Mean for feces[a]		5.04		14.80		50.98		28.59	

[a] Weighted according to the proportions of the two types of feces produced.

dependent upon a conditioning of the gastro-intestinal tract to a high fiber diet and upon the rate at which food passes through the tract. Since the Spruce Grouse used in our experiments probably were not conditioned fully to a diet of conifer needles (they had received a combination of poultry rations and pine browse prior to the experiment), the same explanation may hold.

The calculated ME in pine needles was compared with the recommended levels used by poultry nutritionists. Energy in commercial feeds can be expressed as metabolizable energy per kilogram. This value calculated for pine needles (1562 Kcal/kg) was compared with the recommended levels used by poultry nutritionists. Domestic fowl can be maintained and even grown on rations having an ME value approaching this level (Hill and Dansky 1954). Using the data in tables 3 and 4, which were recorded when ambient temperatures were below freezing, the daily energy consumption by captive Spruce Grouse was 63 Kcal per day (ME $\times$ dry weight of food consumed per day). McDonald et al. (1966) indicate that a mature domestic fowl of a weight similar to that of Spruce Grouse (575 g) would require approximately 79 Kcal per day for maintenance without thermal stress. Brody (1964) states that a fowl of this size would require only 60 Kcal per day for its basal metabolism. Thus it appears that the rate of energy intake by Spruce Grouse was minimal. However, this level is not unreasonable because the experimental birds led a sedentary existence within the small cages (all grouse used in the feeding experiment were docile and remained relatively inactive during their confinement) and it is unlikely that they were thermally stressed to any extent (Delane 1968).

Protein and minerals. The ratio between metabolizable energy and per cent protein (c/p ratio) is of importance in formulating rations for domestic fowl. The c/p ratio for pine needles, $1562/8.36 = 186.8$, is similar to that of formulated rations for both "finishing" and laying fowl (Morgan and Lewis 1962). The ratio required for simple maintenance would be greater (less protein compared to ME) than this figure, as would the rates for laying grouse because they produce fewer eggs at a slower rate than do domestic fowl. In summary, although pine needles are low in protein, the rate at which they are consumed apparently compensates sufficiently to provide an adequate intake of nitrogen.

Captive grouse appeared to vary in their ability to digest pine needles (table 5). In a bird which is maintaining its weight, the protein assimilated equals that deaminated and excreted, so that the apparent digestibility of protein is near zero. On the average, birds used in the feeding experiments lost weight while on a diet of lodgepole pine needles. This weight loss was reflected in a greater quantity of nitrogen in the droppings than in the food (table 4). The grouse were in negative nitrogen balance because they were consuming an average daily amount of 40.4 g of pine needles per bird, of which only 8.36 per cent or 3.4 g was crude protein. At the same time they were producing 29.5 g of droppings per day containing 14.7 per cent, or 4.3 g, of crude protein. Thus these grouse were losing, on the average, approximately 1 g of body protein per day. It is not known whether this loss resulted from an inability to meet energy demands, thus necessitating the catabolism of body protein, or whether it was in response to some other nutrient deficiency for which the birds were compensating through catabolism of muscle.

TABLE 5. Effect of conditioning gastro-intestinal tract on weight changes in captive Spruce Grouse fed only needles of lodgepole pine and held in sheltered outdoor cages during January 1968 at Edmonton, Alberta.

Group[a]	A	B
No. birds	3	3
Days on needle diet	5–7	7–14
Original wt. (g)		
mean	632	560
range	590–663	507–590
Daily wt. change (g)		
mean	−5.4	−1.7
range	−11.0 to −2.5	−10.3 to +9.6

[a] Group A was maintained in captivity for approximately six months prior to experiment on commercial poultry rations with access to pine browse; Group B for a maximum of two weeks on a combination of poultry ration and pine browse.

The difference in the performance of the two groups of grouse (A and B in table 5) seemed to reflect the extent to which the gastro-intestinal tract was conditioned to the diet of conifer needles. Grouse in Group B had been feeding on conifer needles more heavily for a longer period of time and consequently seemed to be able to extract more nutrients from them than did grouse in Group A. Furthermore, two grouse which had been caught in February and placed directly on a diet of conifer needles, were maintained in captivity for two months with access only to pine needles, soil (for possible grit and mineral needs), and snow. During this period their weight was maintained.

TABLE 6. Amino acid content (% dry wt.) of lodgepole pine needles and the levels of amino acid intake (% dry wt.) required by grouse based on a formula for domestic fowl (Morgan and Lewis 1962).[a]

Amino acid	Present in needles	Estimated Spruce Grouse requirement: Maintenance	Estimated Spruce Grouse requirement: Laying
Lysine	0.37	0.10	0.17
Histidine	0.08	0.04	0.06
Threonine	0.07	0.08	0.12
Valine	0.43	0.12	0.18
Methionine	0.04[c]	0.05	0.08
Methionine and Cystine[b]	–	0.08	0.14
Isoleucine	0.35	0.10	0.17
Leucine	0.56	0.13	0.23
Tyrosine	0.18 }	0.15	0.24
Phenylalanine	0.36 }		
Tryptophan[b]	–	0.02	0.04
Arginine	0.38	–	–
Glycine	0.37	–	–
Alanine	0.41	–	–
Aspartic acid	0.63	–	–
Serine	0.28	–	–
Glutamic acid	0.73	–	–
Proline	0.30	–	–
Total	5.54		

[a] All requirements based on a diet with an ME of 1562 Kcal/kg.
[b] Lost in analysis.
[c] Minimal amounts.

Birds need to ingest certain essential amino acids. Morgan and Lewis (1962) give a formula from which the maintenance and laying requirements for essential amino acids can be calculated. The amount of methionine required is calculated, and from this value the amounts of other essential amino acids are estimated by multiplying by appropriate factors. The maintenance requirement for methionine, calculated for an average non-laying domestic fowl of female Spruce Grouse size (513 g) is 0.05 per cent of the dry weight of the food. In a typical laying grouse of 567 g, producing 9.5 g of eggs and losing 2.7 g of body weight per day (Pendergast 1969), the requirement of methionine was calculated to be 0.08 per cent. The amino acids present in pine needles and requirements based on the above calculations are presented in table 6. The summation of all amino acids analysed gave only 5.54 per cent by weight. This is less than the mean crude protein for the sample of needles analyzed (7.25 per cent), reflecting a loss of some amino acids in the analyses and possible errors inherent in calculating crude protein levels. Assuming that the amino acid requirements of grouse are not vastly different from those of domestic fowl, all amino acids, with the possible exception of methionine, were present in adequate quantities (table 6).

In summary, the low digestibility of energy components in pine needles obliges grouse feeding on them to consume large quantities, on a unit of time basis, to obtain sufficient energy. Because of this high rate of consumption, other nutrients in the food such as protein and minerals, which apparently are relatively more available to the bird, would be assimilated in relatively greater quantities and thus compensate for the low percentages of particular nutrients in certain foods.

DISCUSSION

Moss (1967, 1968) suggests that nitrogen and phosphorus are the most likely elements to be limiting in the diets of Red Grouse and Rock Ptarmigan (*Lagopus mutus*). Pulliainen (1970) has demonstrated selection for nitrogen-rich pine needles by Capercaillie (*Tetrao urogallus*), and by inference it may be the most critical nutritional component in this bird's diet in Finland. It is apparent that Spruce Grouse select between needles of different species of conifers and between old and young needles of spruce (Pendergast and Boag 1970), but we have been unable to demonstrate any selection for nitrogen-rich needles by this grouse. Of a series of samples selected by grouse or collected by hand in the field, the sample with the lowest protein content (4.41 per cent) was taken from a grouse. The needles in this sample, taken in December, were yellowish, as if from an unhealthy tree. This suggests that selection of conifer needles by Spruce Grouse is based on criteria other than nitrogen content, perhaps color or texture. Furthermore, the results of the digestive studies suggest that nitrogen is not limiting and therefore Spruce Grouse need not be selective.

The fact that Spruce Grouse can use the needles of conifers as food has provided them with a virtually unlimited food supply wherever these trees dominate the forest. The fact that lodgepole pine is a preferred species in Alberta (Pendergast and Boag 1970) suggests that Spruce Grouse may be closely associated with such a fire-induced disclimax. It remains to be established whether densities decline as succession continues. Pine is not essential, however, for in certain parts of their range, pine is unavailable, yet Spruce Grouse maintain themselves equally well on spruce (Ellison 1966).

There is no evidence to suggest that a change in the level of protein occurs with increasing age of pine trees, that is, time since the last fire (Boag and Kiceniuk 1968), nor that Spruce Grouse distinguish between protein-rich and -poor needles. Thus, those parts of a pine forest inhabited by Spruce Grouse may be selected for their physiognomic features rather than the nutritional characteristics of their foliage.

One possible dietary problem which Spruce Grouse may face occurs at the time of changeover to the winter diet, particularly for juveniles entering their first winter. The suggestion from the data presented herein is that the degree of adaptation through conditioning of the gastro-intestinal tract, both anatomically and physiologically, is critical to their ability to utilize a diet of conifer needles. It is conceivable that Spruce Grouse which have been living on a diet composed heavily of fruit of such forest floor species as *Vaccinium* and little or no conifer browse, may, when faced with a sudden prolonged period of heavy snow cover, be under considerable stress on the imposed diet of conifer browse. The implications for heavy autumn mortality, particularly in young of the year, and its inherent effect on subsequent breeding populations, needs to be tested.

SUMMARY

This paper presents the results of an investigation of the nutrient content of the major foods eaten by Spruce Grouse in central Alberta, and of the digestion of the winter food, pine needles.

Of the foods analyzed, the gross energy value was greatest for pine needles (5.32 Kcal/g dry weight), as were the levels of crude fiber (42 percent) and lignin (26 per cent). By contrast, their crude protein content was the lowest (8.2 per cent), with the exception of spruce needles (5.8 per cent) and fruit of *Vaccinium vitis-idaea* (5.1 per cent). Levels of nitrogen, calcium, phosphorus, magnesium, potassium, and sodium were all relatively low when compared with recommended levels of these minerals in domestic poultry rations.

Feeding experiments using captive Spruce Grouse enabled us to evaluate the digestibility of pine needles. The calculated metabolizable energy in this food was 1.562 Kcal/g dry weight. This is 29 per cent of the total energy present in the needles. In response to the low level of energy extraction, the grouse ate large volumes of needles to bring their energy intake up to a level comparable with that of domestic fowl. The relatively low level of protein and minerals in pine needles was apparently adequately compensated for by the large volume of needles processed per unit of time. Two Spruce Grouse, caught in the wild in February, were maintained in captivity for two months on a diet of pine needles alone. They maintained body weight and condition over this period.

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