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NUTRITION AND CONDITION OF RUFFED GROUSE DURING THE BREEDING SEASON IN SOUTHWESTERN VIRGINIA[1]

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Abstract. Food habits, diet quality, carcass fat, and reproductive condition of 63 Ruffed Grouse (*Bonasa umbellus*) collected in southwestern Virginia during March and April 1982–1984 were determined. Acorns (*Quercus* spp.) made up 60% of the crop contents of 22 grouse collected in 1982, the spring following a year of high acorn production. Leaves of herbaceous plants and buds of deciduous plants were the primary forages of 41 grouse collected in spring 1983 and 1984. Metabolizable energy estimates for grouse diets ranged from 50–64% and 2.30–2.68 kcal/g of dry matter, and dietary protein ranged from 14.6–17.4%. Fat levels of grouse were greater ($P < 0.05$) in March than April, and females had more ($P < 0.05$) fat than males. Fat levels did not differ ($P > 0.05$) among years; however, fat levels of females tended to be greatest in 1982 when acorns were the primary food used. Mean ovary and oviduct weights and paired testes weights increased ($P < 0.05$) from March to April suggesting that concurrent declines in fat reserves were related to increased reproductive activity.

Key words: Carcass fat; metabolizable energy; dietary protein; Ruffed Grouse; spring nutrition.

INTRODUCTION

Except for limited study of food habits, Ruffed Grouse nutritional ecology during the breeding season is poorly documented. In the southeastern United States, information on grouse food habits and body condition during the breeding and egg-laying period is limited to data from nine grouse collected in April in southwestern Virginia (Norman and Kirkpatrick 1984). Studies have shown that nutrition before and during the breeding season can have a significant effect on reproduction of captive grouse (Beckerton and Middleton 1982, 1983). The objective of the present study was to determine the interrelationships among food habits, diet quality, and carcass fat of Ruffed Grouse during the early part of the breeding period in Virginia.

METHODS

Body and organ measurements and crop contents were obtained from 63 Ruffed Grouse (39 females, 24 males) collected during 1982–1984 in the Jefferson National Forest in Giles and Craig counties, Virginia. This area lies within the Ridge and Valley Province of the Appalachian hardwood subregion (Smith and Linnartz 1980). Elevations in the study area range from approximately 600 to 1,200 m. Mixed oak (*Quercus* spp.) hardwoods are the predominant forest cover and even-age forest management is most common.

A minimum of 20 Ruffed Grouse was collected in the late winter or early spring each year (we attempted to collect 10 during 15–31 March and 10 during 15–30 April). Grouse were collected by driving forest roads and shooting from vehicles. Following collection, crop contents were removed and frozen, and crop-free body weight was measured. Grouse were frozen until later laboratory analysis. Reproductive and digestive tracts were removed, and carcass fat was measured by diethyl ether extraction as described by Servello and Kirkpatrick (1987a). Fat levels were calculated as the percent fat in dry carcass weight (carcass fat), and as a lipid index ([g fat/g fat-free carcass weight] × 100). Ovaries, oviducts, and paired testes were weighed after lightly blotting surface moisture. In two instances, testes were damaged by shot and could not be weighed. Macroscopic counts were made of the number of ovulated follicles and follicles >4 mm in diameter. Age was not determined because of the lack of

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an accurate aging technique for Ruffed Grouse in the spring.

Crop contents were oven-dried at 50°C for 24 hr and then separated into eight forage classes: hard fruits, soft fruits, leaves and flowers of herbaceous plants, ferns, leaves of deciduous woody plants, leaves of evergreen woody plants, buds and twigs, and animal matter. Grit was found in only small amounts and was excluded from the food habits analysis and crop contents dry weight. The dry weight of each forage class in each crop was measured. The most common forage species in each year's sample were identified and their percent occurrence by dry weight in the crop was visually estimated as described by Servello (1985). Annual percentages of forage classes and species in the crops were calculated by the aggregate volume method (Martin et al. 1946), except dry weight was used.

Individual crop contents were recombined and ground to pass a 1-mm screen. Contents of each crop were analyzed for percent neutral detergent solubles (NDS) (Goering and Van Soest 1970), except that sodium sulfite was not used (Mould and Robbins 1981). Amylase treatment was used as described by Robertson and Van Soest (1977). Percent total phenols were measured colorimetrically using gallic acid as a standard (Singleton and Rossi 1965) after a 3-day extraction in a acetone/water solution (70:30). Gross energy (GE) was measured with a Parr adiabatic bomb calorimeter. Percent nitrogen was measured by the Virginia Polytechnic Institute and State University Agronomy Laboratory with a Technicon autoanalyzer after digestion in concentrated sulfuric acid at 450°C. Crude protein was calculated as percent nitrogen × 6.25. When there was insufficient crop material for all analyses, priority was assigned in the following order: NDS, phenols, GE, crude protein.

The percent metabolizable energy (ME) of each crop was calculated from the NDS, total phenols, and the percentage of acorns in the crop contents using the following equation (Servello et al. 1987):

$$ME = 0.87(NDS - \text{phenols}) + 0.18(\%\ \text{acorn meat}) - 5.76$$

The predicted ME per gram of forage dry matter was calculated from % ME and GE (kcal/g).

Monthly values of ME (% and kcal/g), total phenols, and crude protein were expressed as percentages or kcal/g of the aggregate total crop content dry weights for each year or month in order that food habits and nutritional quality data would be directly comparable. A protein-energy ratio (g protein per 100 kcal ME) for the crop contents was calculated for each year or month using the aggregate protein and ME (kcal/g) values.

Sex, month, and year differences in percent carcass fat and lipid index were tested by three-way analysis of variance (ANOVA) using the Statistical Analysis System (Ray et al. 1982). Month and year differences in reproductive measurements were tested by two-way ANOVA. Ovarian weight data were transformed to log values for ANOVA to equalize variances, but unweighted means are presented in tables. Specific differences among years were examined with Tukey's multiple range test with the Kramer modification for unequal sample sizes (Ray et al. 1982). One grouse collected in 1983 was considered an outlier and was not used for nutritional and condition analyses. This bird's crop contained 14 g of acorns, more than seven times the average weight for 1983, a year when acorns were rare in crops. The aggregate method of reporting food habits gives biased results when a large amount of a single foodstuff is found in just one or a few samples (Swanson et al. 1974).

RESULTS

REPRODUCTIVE ORGAN MEASUREMENTS

Oviduct ($P = 0.001$), ovary ($P = 0.001$), and paired testes ($P = 0.04$) weights were greater in April than in March (Table 1). Only oviduct weight was different ($P = 0.01$) among years. Tukey's multiple range test indicated that oviduct weight was greater ($P < 0.05$) in 1982 than 1983. As expected from changes in ovarian weights, follicle counts increased from March to April. Two of 10 females collected in March 1982 had ovulated follicles. By late April, all but one female had initiated egg laying in 1982 and 1983, but in 1984, five of seven had not ovulated.

CARCASS FAT

Carcass fat and lipid index were greater ($P = 0.001$) for females than males, greater ($P \leq 0.011$) in March than April, but did not differ ($P > 0.20$) among years (Table 2). Body weight was not different among years ($P = 0.80$), between months ($P = 0.15$), or between sexes ($P = 0.54$) (Table 2). However, there was a month × sex interaction ($P = 0.001$). Females tended to gain weight

TABLE 1. Gonadal and oviduct weights and follicular data for Ruffed Grouse collected in March–April 1982–1984 in Craig and Giles counties, Virginia.

	Ovarian weight[a]			Oviduct weight[a,b]			Paired testes weight[a]			Number of ovarian follicles					Number females with ovulated follicles
											>4 mm		Ovulated		
	n	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	$\bar{x}$	SE	
1982															
March	10	0.5	0.1	10	1.8	0.4	2	0.5	0.2	10	0.7	0.3	0.2	0.1	2
April	7	9.7	2.5	7	11.4	0.5	3	1.2	0.3	7	3.6	0.8	2.6	0.5	7
1983															
March	3	0.3	0.1	3	0.9	0.6	7	0.7	0.1	3	0		0		0
April	9	6.6	1.6	9	9.8	0.3	2	1.3	0.1	9	2.6	0.6	2.7	0.5	8
1984															
March	3	0.2	0.05	3	0.5	0.2	5	0.9	0.3	3	0		0		0
April	7	5.8	2.2	7	9.4	0.7	3	1.0	0.2	7	3.0	0.8	0.6	0.4	2

[a] Means different between months ($P < 0.05$).
[b] Means different among years ($P < 0.05$). Oviduct weight was greater ($P < 0.05$) in 1982 than 1983 (Tukey's multiple range test).

from March to April, whereas males tended to lose weight.

FOOD HABITS AND DIET QUALITY

Mean dry weight ± SE of the crop contents was 3.4 ± 0.8 g in 1982, 2.4 ± 0.9 g in 1983, and 2.2 ± 0.6 g in 1984. Crop contents were composed primarily of either hard fruits, herbaceous leaves, or buds and twigs (Table 3). Other forage classes occurred in lesser amounts (<7%). Hard fruits were found in 13 of 22 crops and made up 63% of the diet in 1982, but were found in small amounts in only three crops in 1983 and three crops in 1984. Acorn meat made up >94% of the hard fruit found in crops (Servello 1985). Herbaceous leaves and flowers were the most

TABLE 2. Carcass fat (%), lipid index [(g fat/g fat-free carcass weight) × 100], and crop-free body weight (g) of Ruffed Grouse collected in March and April 1982–1984 in Giles and Craig counties, Virginia.

		Carcass fat (%)[a,b]		Lipid index[a,b]		Body weight (g)[c]	
	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
March 1982							
Females	10	22.4	1.3	29.2	2.2	627	12
Males	2	10.7	4.9	12.3	6.2	660	15
April 1982							
Females	7	18.3	1.2	22.6	1.8	677	15
Males	3	5.6	1.5	6.0	1.7	597	25
March 1983							
Females	3	16.0	7.0	20.8	10.7	616	43
Males	6	11.3	1.5	13.0	2.0	597	45
April 1983							
Females	9	14.8	2.1	17.0	3.0	632	10
Males	2	2.4	0.5	2.5	0.6	615	49
March 1984							
Females	3	20.0	4.4	25.9	7.0	618	36
Males	7	7.8	1.9	8.8	2.4	660	29
April 1984							
Females	7	13.8	3.5	17.3	5.2	640	10
Males	3	2.6	0.5	2.7	0.5	617	6

[a] Means different between sexes, $P = 0.001$.
[b] Means different between months, $P \leq 0.011$.
[c] Month × sex interaction, $P = 0.001$.

TABLE 3. Frequency of occurrence (number of crops) and percent dry weight of foods from crops of Ruffed Grouse collected in March and April 1982–1984 in Craig and Giles counties, Virginia.

Forage class	1982 (n = 22)		1983 (n = 20)		1984 (n = 20)	
	Frequency occurrence	% dry weight	Frequency occurrence	% dry weight	Frequency occurrence	% dry weight
Hard fruit	13	63	3	3	3	4
Soft fruit	4	2	0	0	5	5
Herbaceous leaves and flowers	19	16	18	57	16	60
Ferns	9	4	4	2	4	2
Deciduous leaves	7	3	5	2	5	4
Evergreen leaves	4	2	3	3	2	7
Buds and twigs	10	6	8	32	9	19
Animal matter	3	2	1	t[a]	0	0

[a] t = trace (<0.5%).

common forages in crops in all years (occurred in >75% of the crops). Flowers of coltsfoot (*Tussilago farfara*) made up 22% and 20% of the crop contents in 1983 and 1984, respectively, and was the most common herbaceous leaf forage in crops (Servello 1985). Buds and twigs were used the least in 1982 when acorns were abundant. Buds found in crops were typically swelled or partially open with emerging leaves.

Total phenols in crop contents varied from 6.7% in 1982 to 3.5% in 1984 (Table 4). Gross energy was lowest but ME was highest in 1982, the year that acorns were the most common in the crop contents. Metabolizable energy levels were 60% and 2.68 kcal/g in 1982, but only 50–53% and 2.30–2.32 kcal/g in 1983–1984. Protein levels in crop contents varied from 14.6% in 1982 to 17.4% in both 1983 and 1984.

DISCUSSION

REPRODUCTIVE ORGAN MEASUREMENTS

Based on reproductive organ measurements, nearly all female and most male Ruffed Grouse were in prebreeding condition in March and were in the midst of breeding activities during the late April collection period. Some males had large testes in March suggesting that males begin reproductive related changes earlier than females.

CARCASS FAT

The decrease in fat from March to April for both sexes was probably directly related to breeding activities. Development of reproductive organs and initial egg laying may have utilized some fat reserves. Male grouse may spend an increasing amount of time in breeding activities and territorial defense at the expense of foraging as the breeding season progresses.

Similar patterns of fat depletion have been observed in ducks (Anatidae). Mallards (*Anas platyrhynchos*), Wood Ducks (*Aix sponsa*), and Ring-necked Ducks (*Aythya collaris*) lose fat during ovarian follicular growth and egg laying (Krapu 1981, Drobney 1982, Hohman 1986), and reduced feeding and fat reserves have been observed in male Ring-necked Ducks attending mates (Hohman 1986).

Male grouse consistently had lower carcass fat levels than females in the spring. Fat levels of males in the present study were similar to low levels previously reported for spring-collected males in Virginia (Norman and Kirkpatrick 1984) and Ontario, Canada (Thomas et al. 1975). However, in March, mean carcass fat levels of females (16.0–22.4%) were as high or higher than fall and midwinter levels reported in other studies of southeastern grouse populations (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987a) suggesting that female Ruffed Grouse are capable of increasing fat reserves in the early spring just prior to breeding if sufficient food is available. Increases in fat reserves just prior to egg laying have been documented in Wood Ducks and Mallards (Krapu 1981, Drobney 1982).

There may be regional or annual variation in fat levels of prebreeding and breeding Ruffed Grouse. In the present study, mean percent carcass fat levels of females in all years and both months (11.3–22.4%) were greater than the mean fat level (4.8%) of three females collected in spring by Norman and Kirkpatrick (1984). Moreover, these fat levels were nearly two times greater than the fat content of females collected in Ontario,

TABLE 4. Neutral detergent solubles (NDS), total phenols, gross energy (GE), metabolizable energy (ME), crude protein, and protein–energy ratios (P/E) of foods from crops of Ruffed Grouse collected in March and April 1982–1984 in Craig and Giles counties, Virginia.

	1982		1983		1984	
	n	Value	*n*	Value	*n*	Value
NDS (%)	20	74.3	16	70.5	19	66.8
Total phenols (%)	20	6.7	16	4.1	19	3.5
GE (kcal/g)	18	4.21	11	4.42	17	4.49
ME (%)	20	64	16	53	19	50
ME (kcal/g)	18	2.68	11	2.32	17	2.30
Protein (%)	15	14.6	9	17.4	14	17.4
P/E (g protein/100 kcal ME)[a]		5.45		6.07		7.57

[a] Calculated from mean ME (kcal/g) and mean protein (%) values.

Canada in March, April, and May (Thomas et al. 1975). Although no statistical differences in carcass fat indices were found among years in the present study, there was some evidence that annual differences existed. All 17 females collected in March and April 1982 had carcass fat ≥13.8% (15 females had carcass fat ≥17%), whereas in 1983, four of 12 females had fat levels ≤7.6%, and in 1984, four of 10 females had fat levels ≤8.3%. Seven of the eight females with low fat levels were collected in April 1983 or 1984. High fat levels in spring 1982 were likely the result of the high use of acorns by grouse during the preceding months. In typical years, the late winter diet of grouse in the southeast contains large amounts of low quality evergreen leaves (Servello and Kirkpatrick 1987b).

Body weight has been shown to have little usefulness as an index of carcass fat in grouse in either the fall or spring (Servello and Kirkpatrick 1987a). In the present study, trends in mean body weights did not follow trends in mean fat levels due largely to concomitant and offsetting changes in fat and reproductive organ weights in spring.

FOOD HABITS AND DIET QUALITY

The use of leaves of herbaceous plants, and buds with emerging deciduous leaves by Ruffed Grouse in the southeast, differs from the spring food habits of grouse in northern areas where catkins of aspens (*Populus* spp.) have been reported the primary spring forages (Vanderschaegan 1970). Aspen is rare in the predominantly oak forests of the southeastern United States, and, therefore, not available as a food resource. Arboreal feeding by grouse in the present study was limited primarily to use of buds with emerging leaves; however, these buds and leaves may have been taken from the ground.

The fall of 1981 was an exceptional year for hard mast production. Acorn production in the Jefferson National Forest was the highest recorded in 32 years (Virginia Commission of Game and Inland Fisheries 1982). The high occurrence of acorns in the crop contents in 1982 demonstrates that in years of high hard mast production, acorns can constitute a substantial part of the late winter and early spring diet of grouse.

When acorns were not abundant in the crops, the spring diet of Ruffed Grouse had approximately 2.3 kcal/g ME (% ME = 50–53) and 17.4% protein. Protein levels of spring diets in the present study were approximately 1.5–2 times greater than these of fall and winter diets in Virginia (Servello and Kirkpatrick 1987b). Higher protein levels in spring diets were probably the result of the use of herbaceous plants (Servello and Kirkpatrick 1987b) and swelled buds and newly emerging deciduous leaves that are high in protein. Dietary ME (64%, 2.68 kcal/g) in 1982 was nearly 20% higher than in 1983–1984 crops without acorns. Therefore, ME was substantially increased when acorns were the major part of the diet. Herbaceous leaves have a high ME content compared to the evergreen leaves used for late winter food by grouse in Virginia (Servello and Kirkpatrick 1987b), suggesting that an abundance of herbaceous leaves in spring may have been the energy source for high fat levels observed in 1983–1984.

Beckerton and Middleton (1982) found that, in diets containing 3.1–3.5 kcal ME/g, 21% protein resulted in the largest clutch size, egg weight, and greatest egg hatchability for captive Ruffed

Grouse in Ontario, Canada. The adequacy of a diet containing 2.3 kcal ME/g and 17.4% protein for grouse reproduction is unknown. Beckerton and Middleton (1982) tested a 17% protein diet, but it contained 3.30 kcal of ME, nearly 1.5 times higher than the natural spring diet of Ruffed Grouse in Virginia (2.3 kcal ME) making a direct comparison of protein levels questionable. However, 2.3 kcal ME and 18% protein is adequate for domestic turkey reproduction (Menge et al. 1979), and 2.6 kcal ME and 15–16.5% protein meets requirements of laying white leghorn chickens (Scott et al. 1982, p. 94). The lower ME in spring diets of wild grouse in Virginia probably would lower the level of dietary protein (<21%) required to maintain protein intake because grouse would presumably eat more of a low ME food and, thus, acquire more total protein (Scott et al. 1982, p. 82). The P/E ratio of 7.5 found in the present study was nearly 1.5 times higher than the P/E ratio of the 21% protein diet in the study by Beckerton and Middleton (1982) that resulted in the greatest reproductive rate in female Ruffed Grouse in the laboratory. Therefore, assuming that wild grouse from Virginia could find sufficient amounts of food to meet their ME requirements, protein levels in 1983 and 1984 appeared to be satisfactory for reproduction.

Tannin phenols in forages may reduce protein digestibility for grouse (McLeod 1974). Total phenol levels in crop contents were low in 1983 and 1984 probably because phenolics are not common in herbaceous annuals or abundant in new growth (Rhoades and Cates 1976). Protein digestibility could have been reduced in 1982 when acorns formed 60% of the diet because high levels of tannins have been found in acorns of some oak species (Ofcarcik and Burns 1971, Servello 1985), and, in fact, total phenols were relatively high in that year.

The spring diet of Ruffed Grouse in southwestern Virginia appears nutritionally adequate for reproduction. However, the ability of forest habitats in the southeast to supply sufficient amounts of high quality food during the early breeding period may be an important factor determining grouse distribution and abundance. Because the primary spring forage of northern grouse populations (aspen catkins) is found on trees, adequate food supplies may be more evenly distributed in northern forested habitats than are the herbaceous forbs used by grouse in the present study. Abundant growth of high quality herbaceous forbs in Virginia forests may be limited to recently disturbed sites or areas with maintained openings (Servello 1985). An abundance of herbaceous forbs in March may be important for increasing fat reserves of female grouse prior to nesting and providing protein for reproductive needs. Food availability in southeastern forests during the breeding season of Ruffed Grouse needs investigation.

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LITERATURE CITED

BECKERTON, P. R., AND A.L.A. MIDDLETON. 1982. Effects of dietary protein levels on ruffed grouse reproduction. J. Wildl. Manage. 46:569–579.

BECKERTON, P. R., AND A.L.A. MIDDLETON. 1983. Effects of dietary protein levels on body weight, food consumption, and nitrogen balance in Ruffed Grouse. Condor 85:53–60.

DROBNEY, R. D. 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. Condor 84:300–305.

GOERING, H. K., AND P. J. VAN SOEST. 1970. Forage fiber analysis: apparatus, reagents, procedures, and some applications. U.S. Dep. Agric. Agric. Handb. 379.

HOHMAN, W. L. 1986. Changes in body weight and body composition of breeding Ring-necked Ducks (*Aythya collaris*). Auk 103:181–188.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29–38.

MARTIN, A. C., R. M. GENSCH, AND C. P. BROWN. 1946. Alternative methods in upland game bird food analysis. J. Wildl. Manage. 10:8–12.

MCLEOD, M. N. 1974. Plant tannins—their role in forage quality. Nutr. Abstr. Rev. 44:803–815.

MENGE, H., H. T. FORBISH, B. T. WEINLAND, AND E. G. GEIS. 1979. Effects of dietary protein and energy on reproductive performance of turkey hens. Poult. Sci. 58:419–426.

MOULD, E. D., AND C. T. ROBBINS. 1981. Evaluation of detergent analysis in estimating nutritional value of browse. J. Wildl. Manage. 45:937–947.

NORMAN, G. W., AND R. L. KIRKPATRICK. 1984. Foods, nutrition, and condition of Ruffed Grouse in southwestern Virginia. J. Wildl. Manage. 48: 183–187.

OFCARCIK, R. P., AND E. E. BURNS. 1971. Chemical and physical properties of acorns. J. Food Sci. 36: 576–578.

RAY, A. A., K. A. COUNCIL, AND J. P. SALL. 1982. SAS user's guide, 1982 edition. SAS Institute, Raleigh, NC.

RHOADES, D. F., AND R. G. CATES. 1976. Toward a

general theory of plant antiherbivore chemistry. Recent Adv. Phytochem. 10:168–213.

ROBERTSON, J. B., AND P. J. VAN SOEST. 1977. Dietary fiber estimation in concentrate feedstuffs. American Society of Animal Science, 69th meeting. Univ. Wisconsin, Madison (Abstr.), p. 254.

SCOTT, M. L., M. C. NESHEIM, AND R. J. YOUNG. 1982. Nutrition of the chicken. M. L. Scott and Assoc., Ithaca, NY.

SERVELLO, F. A. 1985. Regional variation in the nutritional ecology of ruffed grouse. Ph.D.diss., Virginia Polytechnic Institute and State University, Blacksburg.

SERVELLO, F. A., AND R. L. KIRKPATRICK. 1987a. Fat indices for ruffed grouse. J. Wildl. Manage. 51: 173–177.

SERVELLO, F. A., AND R. L. KIRKPATRICK. 1987b. Regional variation in the nutritional ecology of ruffed grouse. J. Wildl. Manage. 51:749–770.

SERVELLO, F. A., R. L. KIRKPATRICK, AND K. E. WEBB, JR. 1987. Predicting metabolizable energy in the diet of ruffed grouse. J. Wildl. Manage. 51:560–567.

SINGLETON, V. L., AND J. A. ROSSI, JR. 1965. Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. Am. J. Enol. Viticult. 16:144–158.

SMITH, D. W., AND N. E. LINNARTZ. 1980. The southern hardwood region, p. 145–230. *In* J. W. Barrett [ed.], Regional silviculture of the United States. John Wiley and Sons, New York.

SWANSON, G. A., G. L. KRAPU, J. C. BARTONEK, J. R. SERIE, AND D. H. JOHNSON. 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38:302–307.

THOMAS, V. G., H. G. LUMSDEN, AND D. H. PRICE. 1975. Aspects of the winter metabolism of ruffed grouse (*Bonasa umbellus*) with special reference to energy reserves. Can. J. Zool. 53:434–440.

VANDERSCHAEGAN, P. V. 1970. Food habits of ruffed grouse at the Cloquet Forest Research Center, Minnesota. M.S.thesis, Univ. Minnesota, St. Paul.

VIRGINIA COMMISSION OF GAME AND INLAND FISHERIES. 1982. Black bear investigations. Va. Wildl. Investigations Annu. Prog. Rep., Fed. Aid in Wildl. Restoration Proj. W65-W71-R-2 and EW-1-6.