THE AUTUMN DIET OF SPRUCE GROUSE: A REGIONAL COMPARISON

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Spruce Grouse (Canachites canadensis) are distributed across much of northern North America (Aldrich 1963). In recent years several workers have reported on the autumn or year-round food habits of this species in widely separated regions of the continent (Crichton 1963, in Ontario; Jonkel and Greer 1963, in Montana; Ellison 1966, in Alaska; Pendergast and Boag 1970, in Alberta). During September and early October of 1957 through 1961, we collected 113 crops from Franklin's Spruce Grouse (C. c. franklinii) in north-central Washington. In this note, we compare quantitative and qualitative characteristics of the contents of these crops to similar data for Spruce Grouse from other regions, and to similar data for Blue Grouse (Dendragapus obscurus) in the same region from which our samples were collected.

All crops were taken from birds shot by hunters. Samples were collected at a checking station near the boundary of a 100 square mile study area in the Conconully region of north-central Washington (see Zwickel et al. 1966). Crop contents were preserved in formalin and analyzed wet.

RESULTS AND DISCUSSION

Food habits may vary among years within an area (Boag 1963). Generally, our data indicated that there were no differences in the autumn diet of Spruce Grouse in the Conconully area between 1960 and 1961, the 2 years in which most of our collections were made (table 1). Thus, we combined our data from different years into one larger sample.

We determined age and sex for practically all Spruce Grouse from which crops were obtained (Zwickel and Brigham 1970). Since Boag (1963) has shown that there may be differences in food habits of Blue Grouse among different age-sex groups, we compiled our data by age and sex of the birds from which they were collected. Chi-square analyses of frequency of occurrence of the major items, lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), huckleberries (*Vaccinium spp.*), and grit all showed no significant differences ($\tilde{P} < 0.05$) among the various age-sex groups. Student's t-test was used for volumetric comparisons of the same items (except grit) and also showed no significant differences. We therefore combined data for all birds (table 1) and consider that the results are generally representative of the autumn diet of Franklin's Spruce Grouse in this area.

At least 29 genera of plants and 3 genera of animals occurred in the diet of birds examined. The major items in the diet were lodgepole pine, larch, and huckleberry, in that approximate order. The quantity of lodgepole pine was approximately three times that of the next most abundant species, larch. Others have also found conifers of one species or another to be the major components in the autumn diet of Spruce Grouse (Crichton 1963; Jonkel and Greer 1963; Ellison 1966; Pendergast and Boag 1970).

The species of conifers used most heavily in a given area may vary likely, in part, in relation to availability. For example, the main conifers present in Ellison's area were spruces (Picea spp.) and he reported them to be the major items used by Spruce Grouse in autumn (data from September and October combined by us for comparison to our data). Additionally, Jonkel and Greer reported much more larch than pine in the autumn diet of birds they examined, the opposite of our findings in Washington. Pendergast and Boag reported that lodgepole pine and spruce were the two main items found in birds from Alberta. Hence, as a species, Spruce Grouse appear relatively adaptable with respect to major species of foods used in autumn, yet are closely associated with one major group of trees, conifers.

Data presented by Ellison (1966) and Pendergast and Boag (1970) indicate that the amount of conifer browse in the summer diet of Spruce Grouse is much lower than in autumn. All studies with data from winter indicate that the diet then is almost exclusively conifer browse. Clearly, autumn is a period of transition from a mainly nonconiferous diet to one composed almost solely of conifer needles. At the same time, results from all studies indicate that huckleberries especially and other understory plants continue to make up a large part of the diet at this time of year.

A coniferous diet may be adaptively related to availability in snowy areas. However, all studies show that the shift to this diet is occurring long before snowfall might make other foods unavailable. Four possible, but not necessarily exclusive, explanations for this early seasonal shift to conifers can be suggested: (1) the birds must shift to the winter diet gradually; (2) alternative foods are declining in availability, or quality, or both; (3) this shift represents preference; or (4) some behavioral change is occurring that is unrelated to food but that results in more time being spent in trees than on the ground.

Our data suggest a species diversity in the autumn diet—at least 29 genera of plants—that is comparable to that reported for Spruce Grouse in northwest Montana (Jonkel and Greer 1963) and Alaska (Ellison 1966). Pendergast and Boag (1970), however, reported only 18 genera of plants in the autumn diet of Spruce Grouse in the Swan Hills of central Alberta, and Crichton (1963) reported that only 11 genera were found in central Ontario. Perhaps dietary diversity is lower in the broad belt of continental boreal forest as compared to coastal (Alaska) or montane regions (Montana and Washington). At any rate, the diversity of plants in the diet may vary widely from region to region, again suggesting flexibility in the feeding habits of Spruce Grouse.

Pendergast and Boag (1970) reported a higher diversity in the autumn diet of juveniles than in adults. They suggested that this might be explained by a difference in the size of their samples for the two age groups. In our samples, which were more comparable between age groups, adults had eaten 20 genera of plants and juveniles, 21. Hence, the difference reported by Pendergast and Boag was likely related to sample size.

Franklin's Spruce Grouse and Blue Grouse occur sympatrically in the Conconully area. Boag (1963) has reported on the food habits of Blue Grouse in this region. He found at least 51 genera of plants

	Parts eaten	Vol.c,d	$\mathbf{v}_{\mathrm{ol.}}^{\%}$	Freq. occ.	% Occ.
lants					
Pinus contorta	Needles	240.5	47	59	52
Larix occidentalis	Needles	81.5	16	26	23
Vaccinium spp.	Fruit	42.0	8	25	22
	Leaves and stems	31.0	6	49	43
Arctostaphylos uva-ursi	Fruit	23.5	5	10	9
Actea arguta	Fruit	20.0	4	3	3
Trifolium sp.	Leaves	16.0	3	15	13
Pseudotsuga menziesii	Seeds	13.0	3	13	12
	Needles	2.5	<1	1	<1
Picea engelmanni	Needles	10.0	2	3	$<1 \\ 3 \\ 5 \\ <1 \\ 4 \\ 9$
Taraxacum sp.	Leaves	5.0	1	6	5
Lactuca sp.	Flowers	5.0	1	1	<1
Hieracium sp.	Flowers	3.5	< 1	4	4
Arceuthobium sp.	Stems and fruit	3.5	< 1	10	9
Symphoricarpos [°] albus	Fruit	3.0	<1	1	< 1
Epilobium sp.	Fruit	1.5	<1	1	<1
Pinus ponderosa	Needles	1.0	<1	1	<1
Ribes sp.	Leaves	1.0	<1 < 1 < 1 < 1	5	4
Eubasidiomycetes	Sporophore	1.0	<1	5	4
Antennaria sp.	Leaves	1.0	$\langle 1$	2	2
Agoseris sp.	Leaves	0.5	<1	1	< 1
Unidplant	Leaves	0.5	<1	3	3 5
Stellaria sp.	Leaves	t		6	5
Pedicularis sp.	Leaves	t		4	4
Fragaria sp.	Leaves	t		2	2
Rumex sp.	Leaves	t		1	< 1
Lupinus sp.	Seeds	t		1	<1
Carex sp.	Spikes	t		1	<1
Anemone sp.	Leaves	t		1	$\langle 1$
Gramineae	Leaves	t		1	<1 < 1 < 1
Unid. moss	Leaf	t		1	< 1
Animals					
Formicidae		t		10	9
Geometridae		t		2	2
Diptera		t		1	< 1
Grit		2.5	1	28	25

TABLE 1. Contents of 113 Spruce Grouse crops from Conconully, Washington-all age-sex classes^a and years^b combined.

* Numbers of crops from each age-sex class were as follows: adult male-22, adult female-24, juvenile male-27, juvenile ^b Crops were collected in the following years: 1957 to 1959—5, 1960—24, 1961—84. ^c Volume is in m1 of water displacement. ^d t = trace (<0.25 m]). female-38, unknown-2.

and 14 genera of animals in 602 crops examined. The greater diversity in the diet of Blue than Spruce Grouse in this region may be related to a much larger sample size from Blue Grouse. However, it is more likely related to specific habitat types used by the two species. Spruce Grouse are found, throughout the year, mainly in stands with a high proportion of lodgepole pine. This appears to be the habitat type least used by Blue Grouse. In autumn, however, Blue Grouse are found throughout the area, from the wheatgrass-bluegrass zone (Daubenmire 1946) to alpine tundra.

A general habitat separation between the two species of grouse also can be seen by comparing the major foods utilized by them in the Conconully area in autumn. Lodgepole pine and larch are most used by Spruce Grouse, but larch and Douglas fir (Pseudotsuga menziesii) are used by Blue Grouse. Hence, there is some separation in food habits, but it is incomplete, as also suggested by comparing other items in the diet of the two species. Perhaps features of the habitat other than food are most important in causing the spatial separation of the two species during much of the year.

Several employees of the State of Washington Department of Game assisted with the collection of data. J. Ganaway, Department of Zoology, Washington State University, assisted with the analysis of crop contents. D. A. Boag analyzed many of the crop contents while associated with the Department of Zoology, Washington State University. F. C. Zwickel was an employee of the Washington Department of Game when many of the crops were collected.

LITERATURE CITED

- ALDRICH, J. W. 1963. Geographic orientation of American Tetraonidae. J. Wildl. Mgmt. 27:529-545.
- BOAG, D. A. 1963. Significance of location, year, sex, and age to the autumn diet of Blue Grouse. I. Wildl. Mgmt. 27:555-562.

- CRICHTON, V. 1963. Autumn and winter foods of the Spruce Crouse in central Ontario. J. Wildl. Mgmt. 27:597.
- DAUBENMIRE, R. F. 1946. The life zone problem in the northern intermountain region. Northwest Sci. 20:28-38.
- ELLISON, L. 1966. Seasonal foods and chemical analysis of winter diet of Alaskan Spruce Grouse. J. Wildl. Mgmt. 27:729–735.
- JONKEL, C. J., AND K. R. GREER. 1963. Fall food habits of Spruce Grouse in northwest Montana. J. Wildl. Mgmt. 27:593-596.

FLIGHT DISPLAYS IN TWO AMERICAN SPECIES OF BUTEO

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Flight displays occur widely among birds of prey (Brown and Amadon, Eagles, hawks, and falcons of the world, p. 95–101. McGraw-Hill, New York. 1968). A common type of courtship display is a circling flight in which the male (typically) stoops on the female, with actual or symbolic foot-touching occurring when she turns on her back to meet him at the moment of contact or near contact. Another version involves a prolonged grasping of the feet by the two birds, followed by a spectacular tumbling earthward. The latter behavior is known to occur in various eagles (especially *Haliaeetus*), some kites (*Haliastur, Milvus*), and in the Upland Buzzard (*Buteo hemilasius*) of Asia.

Several years ago I observed flight displays in two species of *Buteo* in New Mexico, one involving courting Red-tailed Hawks (*B. jamaicensis*) and the other, Zone-tailed Hawks (*B. albonotatus*). The display seen in *B. jamaicensis* involved the use of a snake and that in *B. albonotatus* a tumbling fall, features that do not seem to have been reported before in these species.

My observations of courtship flight in *B. jamaicen*sis agree in most respects with those reported previously (e.g., Fitch et al., Condor 48:209, 1946; Austing, The world of the Red-tailed Hawk. J. B. Lippincott Co., Philadelphia and New York, p. 39-41, 1964). The birds seen by me near Silver City, Grant County, on 30 April 1961, were both adults of the pale *fuertesi*-like breeding population of southern New Mexico. The two birds differed notably in size, and I assume that the smaller was the male. I watched them for about 15 min as they circled overhead, the male ranging from about the same level to perhaps 20 ft above the female. Their flight was leisurely and flat-winged, with the male generally circling behind and above the female as they performed spirals of up to 100 ft in width. In his talons the male carried a limp snake, some 2 ft long and of an unidentified species. Perhaps 10 times during the period the male circled above the female and then with quickened wingbeats he swooped down at her, trailing the snake by her as she turned over to meet him. In no instance did she actually succeed in grasping the snake, although the male came within 3 ft of her on several occasions before turning to rise again. All through the performance at least one of the birds uttered a loud, low and

- PENDERGAST, B. A., AND D. A. BOAC. 1970. Seasonal changes in diet of Spruce Grouse in central Alberta. J. Wildl. Mgmt. 34:605-611.
- 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 J. H. BRIGHAM. 1970. Autumn sex and age ratios of Spruce Grouse in northcentral Washington. J. Wildl. Mgmt. 34:218– 219.

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raspy *hrrr*, *hrrr*, *quite* unlike the ordinary scream of the species. This call apparently is the same as that described as *chwirk* by Fitch et al. (op. cit.), who also noted it during courtship flights. Eventually the two birds moved out of sight, still circling and displaying at about the same height.

Some indication of the function of this behavior is suggested in Brown and Amadon's discussion of sexual dimorphism and its significance in raptors (op. cit., p. 26–28). Among many species the female is notably larger than the male and, of all the theories put forward, these authors favor one that points to this as facilitating pairing. They explain that in species that are aggressive and usually solitary, what amounts to a conflict of drives may occur when birds come together to breed. These drives are predation and reproduction. The assumption is made that because the female is larger, the male is cowed in its predatory drive while remaining stimulated in its sexual drive.

Of course, the female must be receptive to the sexual advances of the male, or her predatory drive may end up inhibiting or preventing reproduction. Thus it would seem necessary that an interplay of signals takes place to insure pairing and breeding. In this regard, it may be that the larger female communicates a willingness to breed by allowing the male to dominate her in certain respects. For example, in the courtship flight of B. jamaicensis the male appears to be the aggressor, with the female covering up in response to his stooping. Brown and Amadon (op. cit.) also mention the courtship feeding of the female by the male in various raptors, an activity that they postulate may reduce or eliminate potential hostility. This behavior may also be another signal to the male of the female's receptiveness to breed, and it could also be a stimulus leading toward his later role of feeding the incubating female and then the young.

In certain respects the behavior of the female during the early breeding cycle recalls that of young birds—as is the case in many nonraptors, including being fed and wing-fluttering (associated with copulation). In *B. jamaicensis* the female has been known to elicit copulation while giving the begging call of the young (Fitch et al., op. cit.), and her nondomination of the courting male may be another "regressive" signal. Furthermore, I suggest that my observation of snake-carrying during courtship flight also fits this pattern, and in fact it may represent courtship feeding at some stage. One could even extend the argument by saying that, as with adults luring young with food, the male may have been manipulating the female—perhaps even toward the nesting area. The stage of breeding of the birds I