Am. Midl. Nat. 136:157-171

Feeding Ecology of Merriam's Turkeys (Meleagris gallopavo merriami) in the Black Hills, South Dakota

MARK A. RUMBLE

U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, 501 East St. Joseph, Rapid City, South Dakota 57701

AND

STANLEY H. ANDERSON

U.S. Department of Interior; Fish and Wildlife Service, Cooperative Fish and Wildlife Research Unit, Department of Zoology, University of Wyoming, Laramie 82071

ABSTRACT- We studied the feeding ecology of Merriam's turkey *(Meleagris gallopavo merriami)* in the Black Hills, South Dakota, between 1986 and 1989. Adult birds consumed 78 kinds of food, of which four food categories constituted >79% of winter diets and six food categories constituted >75% of summer diets. Ponderosa pine *(Pinus ponderosa)* seeds were the preferred winter food and birds selected habitats where pine seed abundance was highest. During drought, ponderosa pine produced fewer seeds and winter turkey diets were predominantly kinnikinnick *(Arctostaphylos uva-ursi)* fruits and herbaceous foliage and seeds. Merriam's turkeys consumed more green foliage from late winter through spring. Summer diets were mostly grass seeds and foliage. Arthropods comprised >60% of the poult diets. Poults ≤3 wk old consumed more arthropods than poults >7 wk old. Grasshoppers (Orthoptera) and beetles (Coleoptera) were the primary arthropods eaten by poults. Brood hens selected macrohabitats where arthropod abundance was highest. Poults selected arthropods with large mass/individual and disregarded some arthropods that were abundant but with low mass/individual.

INTRODUCTION

Obtaining nutritious food is an important aspect of wild turkey ecology (Hurst, 1992). Understanding the ecological relationships between subspecies of wild turkeys (*Meleagris gallopavo)* must include evaluations of feeding ecology of subspecies. Useful comparisons of wild turkey diets rely on well-balanced knowledge of the foods consumed in relation to their availability. To date, the feeding ecology of Merriam's turkey *(M. g. merriami)* remains largely unknown despite considerable research on other subspecies of wild turkeys over several decades.

Most information about the foods of Merriam's turkeys was collected during hunting seasons, when food resources rarely limit game bird populations (Gullion, 1966). Merriam's turkeys are considered opportunistic omnivores (Hurst, 1992). Grasses, grass seeds, ponderosa pine *(Pinus ponderosa)* seeds, kinnikinnick *(Arctostaphylos uva-ursi)* fruit and invertebrates are common foods of Merriam's turkeys (Scott and Boeker, 1973; Petersen and Richardson, 1975; Schemnitz et al., 1985) but these studies contained no measurements of food availability. Only limited research, during winter, compared diets of Merriam's turkeys to food availability (Wakeling and Rogers, in press). Unlike eastern turkeys, Merriam's turkeys do not rely on acorns (Quercus spp.) as a staple food (Scott and Boeker, 1973; Petersen and Richardson, 1975; Laudenslager and Flake, 1987). Foods of poults wk old for all subspecies of wild turkeys are largely unknown (Hurst, 1992).

Our objectives were to quantify eating habits, food availability and selection of foods by Merriam's wild turkeys in a mostly ponderosa pine forest. Specifically, we wanted to investigate temporal and spatial variation in turkey diets compared to seasonal availability of foods.

STUDY AREA AND METHODS

We conducted this study from March 1986 to March 1989. Our study area of 4380 ha is 16 km W of Rapid City, South Dakota. The vegetation is mostly ponderosa pine forest (84%), with meadows (10%), quaking aspen (*Populus tremuloides)* /paper birch *(Betula Papyrifera) (5%)* bur oak (*Quercus macrocar-a) (*< 1%) and white spruce *(Picea glauca* (<1 %). Elevation ranges from 1300 to 1800 m. Climate is continental with cold winters (- 11 to 2 C) and warm summers (15 to 29 C) (0rr, 1959). Annual precipitation from 1956 to 1990 averaged 50.5 cm (data from 1977-1979 missing, South Dakota Climatological Summary, U.S. Dep. Comm., Asheville, N.C.).

SAMPLING METHODS

Diet samples.- W e collected fresh fecal droppings from roosts and diurnal locations of 36 female (18 were brood hens) and eight male radio-marked turkeys. Thirteen birds were radio-marked the 1st winter representing approximately 60% of the population in the area. We radio-marked ≥20 birds during the winters of 1987 and 1988, which comprised approximately 50% and 25% of the populations, respectively. We collected droppings at roosts 1-2 mornings each week and when encountered during daily field work. Fecal samples that occurred in flocks with radio-marked birds included droppings from unmarked turkeys. Microhabitats and diets of Merriam's turkeys are generally similar between sexes (Rumble and Anderson, 1996; Wakeling and Rogers, in press). Therefore, we did not attempt to differentiate dietary differences among sexes of bird that occurred in flocks with our radio-marked birds. Droppings were placed in envelopes, labeled and oven-dried at 60 C for ≥1 wk.

We combined all adult turkey droppings into samples representing 1-wk intervals of each year of the study (Lewis, 1994). Nutritional requirements and diets of poults vary with age (National Research Council, 1977; Hurst, 1992). Therefore, fecal droppings from poults (≤12 weeks of age) were pooled into samples representing l-week age categories for each year.

The relative frequency of arthropod orders in each fecal sample was determined from 40 fields examined at 40x in a petri dish. Each sample was then ground to pass a 20 mm mesh screen and five slides were prepared. Examination of 20 fields per slide (100 fields per sample) at 100x was used to estimate percent composition for total arthropods and other diet components (Sparks and Malachek, 1968; Havstad and Donart, 1978). Percent composition of arthropod orders in each sample was then estimated by multiplying the relative frequency from the 40x examination by the percent of total arthropods from the 100x examination. Pine seed and acorn composition in diets were adjusted to account for underestimation of these foods using the microscopic fecal technique (Rumble and Anderson, 1993a). We provided reference specimen lists of probable turkey foods to the technician reading the slides. The technician reading our samples is highly skilled and reads slides full-time. An independent test using the same technician showed that after correcting for mast items, composition errors were ≤5% of hand-compounded diets (Rumble and Anderson, 1993a). Microscopic fecal analyses may underestimate soft-bodied invertebrates in diets (Dickman and Huang, 1988). We do not believe soft-bodied arthropods were severely underestimated because soft-bodied arthropods were not common in field samples

used to estimate availability of arthropods and because undigestible body parts, such as mandibles, of soft-bodied arthropods were rare in diets estimates. Under these conditions, fecal analysis provides accurate quantitative diet estimates (Marti, 1982).

Food availability.- We sampled to estimate abundance of turkey foods at 52 sites classified by vegetation community (VEG) and overstory cover (OCC). These sites were initially selected using visual estimates; OCC was later measured using a spherical densiometer (Lemmon, 1956; Griffing, 1985) at three locations 15 m apart, at each site. Sites included aspen/birch (n = 14), meadow centers (n = 5), meadow edges (n = 5), ponderosa pine 0-40% OCC (n = 6), ponderosa pine 41-70% OCC (n = 16) and ponderosa pine 71-100% OCC (n = 6). Sites selected for sampling abundance of turkey foods were subjectively distributed throughout the study area. Meadow edges were differentiated from meadow centers because hens with poults typically feed along forest-meadow edges (Jonas, 1966). The unequal sample sizes resulted from initial visual estimates of OCC that were later quantified, initial classification that included diameter at breast height (DBH) of trees but that were later combined (Rumble and Anderson, 1992) and some food availability sites that were destroyed by logging. We measured tree basal area at each site using a lo-factor prism (Sharpe *et al.*, 19'76).

During June 1987, we clipped all vegetation in three 0.5-m^2 circular plots spaced 10 m apart along a 20-m transect at each food availability site. Clipped vegetation was placed in paper bags, air-dried at 60 C for ≥1 wk and weighed. Along the same transect, we estimated percent canopy cover in six cover classes (Daubenmire, 1959) for grasses, forbs and shrubs in 20, 0.1 m2 quadrats spaced at l-m intervals. Percent canopy cover of these categories provides an index to biomass (Payne, 1974; Humphrey, 1985). Therefore, we partitioned total biomass into categories of biomass for grasses, forbs and shrubs by multiplying relative percent canopy cover of these categories times total biomass from clipped plots.

On 1 September 1987 and 1988, we placed three, 0.5-m^2 circular plots with nylon screens on the ground spaced 10 m apart at each food availability site. These screens were collected and seeds were counted on 29-31 October, before opening of the firearm deer season. Because these screens were not animal-proof, we included seed wings in our counts of ponderosa pine seeds.

Arthropod abundance was estimated at each of these sites using a sweep net. During June and July of 1987 and 1988, 45 passes of a sweep net were made while walking through the vegetation at the site. One pass of the net consisted of a forehand or backhand stroke. All of these samples were collected on the same day each month between 0700 and 1600 h by the first author. Contents of sweep nets were placed in plastic bags and frozen. Contents of samples were later identified to order, counted, air-dried at 60 C for ≥1 wk and weighed.

DATA ANALYSIS

We tested our data for homogeneity of variances and normality. The assumptions of parametric statistical tests were seldom met. We used analytical methods that did not require these assumptions or that included adjustments in the calculations to account for the violation of these assumptions.

Food availability.- We used two-way analysis of variance for heterogeneous variances (Brown and Forsythe, 19'74) to test the hypothesis that ponderosa pine seed abundance did not differ among years and VEG/OCC categories. The year-by-VEG/OCC interaction in this test was significant, so we conducted multiple range tests separately for each year using Welch's test and Dunnett's T3 procedure for heterogeneous variances (Dunnett, 1980; liken and Johnson, 1984).

We used Spearman's rank correlation to explore relationships between ponderosa pine

seed availability and ponderosa pine basal area among sites. To facilitate visual depiction of the relationships between ponderosa pine seed production and basal area we aggregated these data to the VEG / OCC categories and used nonlinear and linear regression to show how pine seed production varied with basal area between the 2 yr. When data are aggregated, average values are more normally distributed (Dixon and Massey, 1969:324). Nonetheless, appropriate use of these regression relationships are qualitative and we do not present the regression equations.

We tested the hypothesis that understory vegetation and arthropod abundance did not differ among VEG / OCC categories using multiresponse permutation procedures (MRPP) described by Mielke (1984). We used Spearman's rank correlation to explore relationships between arthropod abundance and herbaceous biomass.

Diets.-Food items that occurred in < 10% of samples or that averaged <1% of diets among individual samples were aggregated into categories such as grass foliage, grass seeds, forb foliage, forb seeds / flowers, etc. We assumed the growing season in the Black Hills begins 1 May. Snow was uncommon after this date and plants broke dormancy. For adult turkeys, we designated 1 May to 30 September as the summer diet period and October to April as the winter diet period based on patterns of microhabitat selection (Rumble and Anderson, 1996). Within each season, we used MRPP to test the hypothesis that major diet components did not differ among growing seasons. Spearman's rank correlation was used to evaluate the relationships between major winter diet components.

We categorized poult diet samples into poult age classes of O-3, 4-7 and 8-12 wk. Protein requirements decline with age of poults, and poult diet patterns of other wild turkey subspecies suggested this classification (Leopold, 1943; Robbins, 1983; Hurst, 1992). MRPP was used to test the hypothesis that foods eaten by poults did not differ among age classes of poults.

Turkey poults have high protein requirements for their 1st 7 wk (National Research Council, 1977; Robbins, 1983), and they meet these requirements by consuming invertebrates (Hurst and Poe, 1985). We evaluated selection of arthropods in diets of poults O-3 and 47 wk old using Spearman's rank correlations. First, we evaluated the relationships between biomass of arthropods from sweep net samples and arthropod composition in diets of poults. We then determined if poults selectively consumed arthropods based on size, using rank correlations between mass / individual of arthropods and arthropod composition in diets of poults. We determined whether size (mass / individual) of arthropods was related to biomass of arthropods available to poults using rank correlations. Finally, we determined the relationships between consumption of grasshoppers (largest mass / individual) and consumption of smaller arthropods by poults using rank correlations.

We choose $\alpha \leq 0.10$ for accepting statistical significance. All tests protected for experiment-wise error rates at this level. This study was designed to evaluate patterns of habitat and diet selection in a variable environment. The consequences of type I errors were low, but consequences of type II errors (e.g., random patterns of selection and few potential effects on turkey populations resulting from forest management) caused us to choose $\alpha \leq 0.10$ for determining significance in statistical tests. Names of plants follow Flora of the Great Plains (Great Plains Flora Association, 1986).

RESULTS

ADULT DIETS

Adult turkeys consumed 78 kinds of food, but 12 constituted 95% of diets (Fig. 1). Ponderosa pine seeds, kinnikinnick fruit, Kentucky bluegrass (*Poa pratensis*) and corn (*Zea*

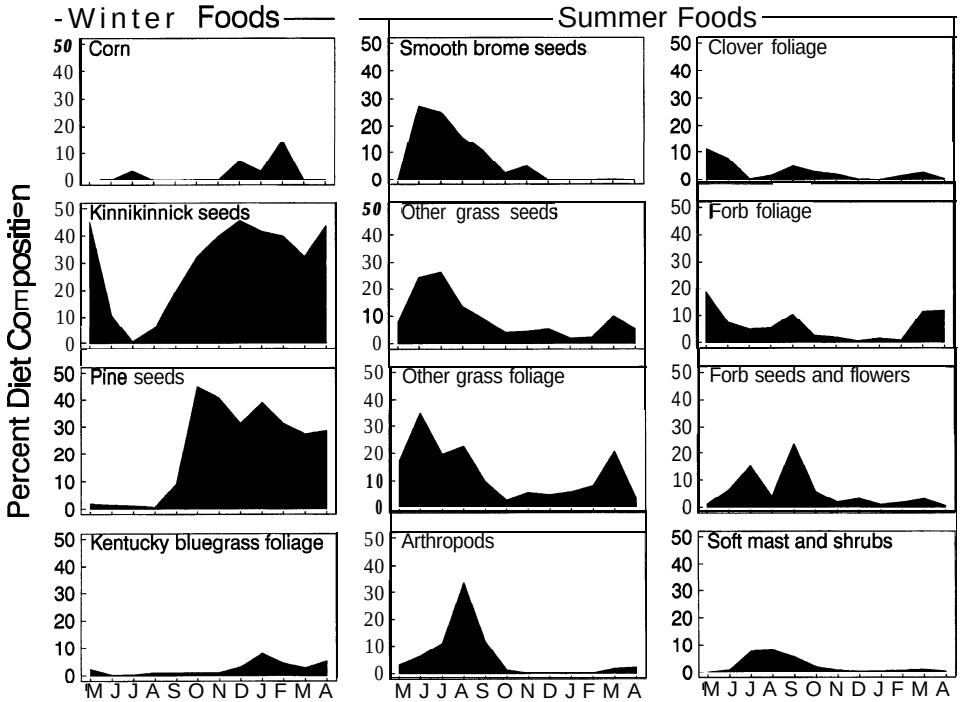

FIG. l.-Average monthly percent composition based on dry matter intake of 12 food items or categories for Merriam's turkeys 1986-1988

mays) were the primary winter foods, comprising '79% of October-to-April diets. Ranked composition of pine seeds and kinnikinnick fruits in winter turkey diets were negatively correlated ($r = -0.8$, $P \leq 0.01$). Grass and forb foliage, grass seeds and forb seeds/flowers comprised increasingly large proportions of turkey diets from late winter through spring. Kinnikinnick fruits remained high in turkey diets during May, but herbaceous foliage, grass seed, forb seed/flowers and arthropods were the primary May-to-September foods of adult turkeys. Grass foliage and seeds, primarily smooth brome *(Bromus inermis)* seeds, dominated diets from June through September. The proportion of arthropods consumed by adult turkeys increased during early summer and declined after August. Soft mast appeared in turkey diets only during midsummer. Peak consumption of forb seeds/flowers coincided with spring and autumn periods of flowering.

Annual variation within seasons.-Summer diets varied annually and monthly (Fig. 2). Consumption of clover *(Trifolium* spp.) and other forbs did not differ among years; these food items averaged 5.3% and 5.7%, respectively, in summer diets. Smooth brome seeds comprised a significantly lower ($P = 0.01$) proportion of turkey diets during 1988 [5.6 ± 3.9% ($\bar{x} \pm SE$)] than during 1986 (26.3 ± 6.5%). Turkeys consumed more ($P = 0.05$) grass seeds other than smooth brome in 1987 (24.7 ± 4.7%) than during 1988 (10.2 ± 3.9%). Foliage of grasses was consumed more ($P = 0.08$) during 1986 (8.2 ± 1.2%) and 1987 (11.6 ± 3.7%) than during 1988 (3.5 ± 0.8%). Adult turkeys consumed fewer ($P = 0.07$) arthropods in 1986 (7.7 ± 1.6%) than during 1988 (21.1 ± 6.5%). During 1986, turkeys consumed more ($P = 0.09$) forb seeds/flowers (13.8 ± 3.3%) than during 1987 (5.3 ±

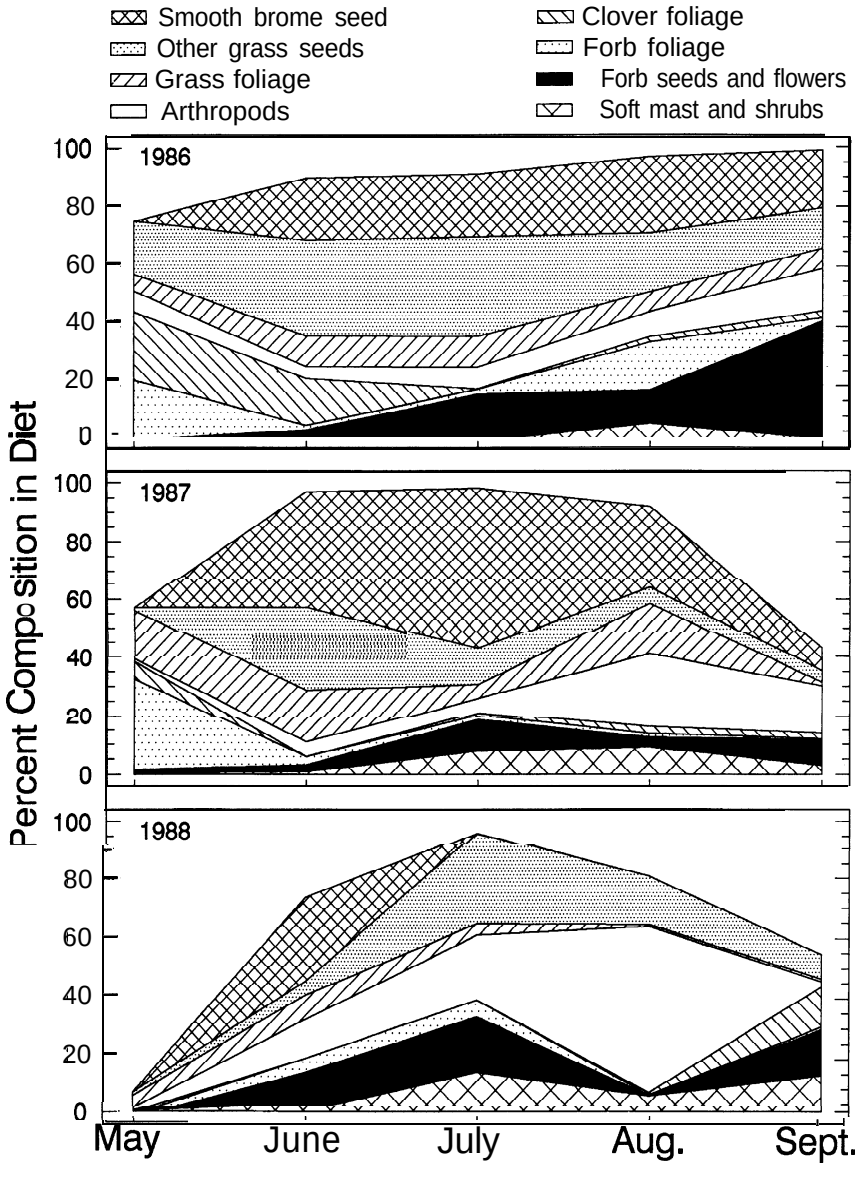

FIG. Z.-Cumulative percent composition of May-September turkey diets 19861989

1.4%). Although soft mast and shrubs in diets differed among years ($P = 0.06$), no pairwise differences were discernible in multiple range tests.

Turkeys ate fewer ($P \leq 0.01$) pine seeds during winter 1988-1989 ($9.2 \pm 4.4\%$) than 1986-1987 ($52.1 \pm 4.4\%$) or 1987-1988 ($40.0 \pm 4.6\%$), as shown in Figure 3. Consumption of kinnikinnick fruits during winter ($\bar{x} = 38.9\%$) did not differ ($P = 0.15$) among years. Turkeys consumed more ($P \leq 0.03$) Kentucky bluegrass during successive winters of our

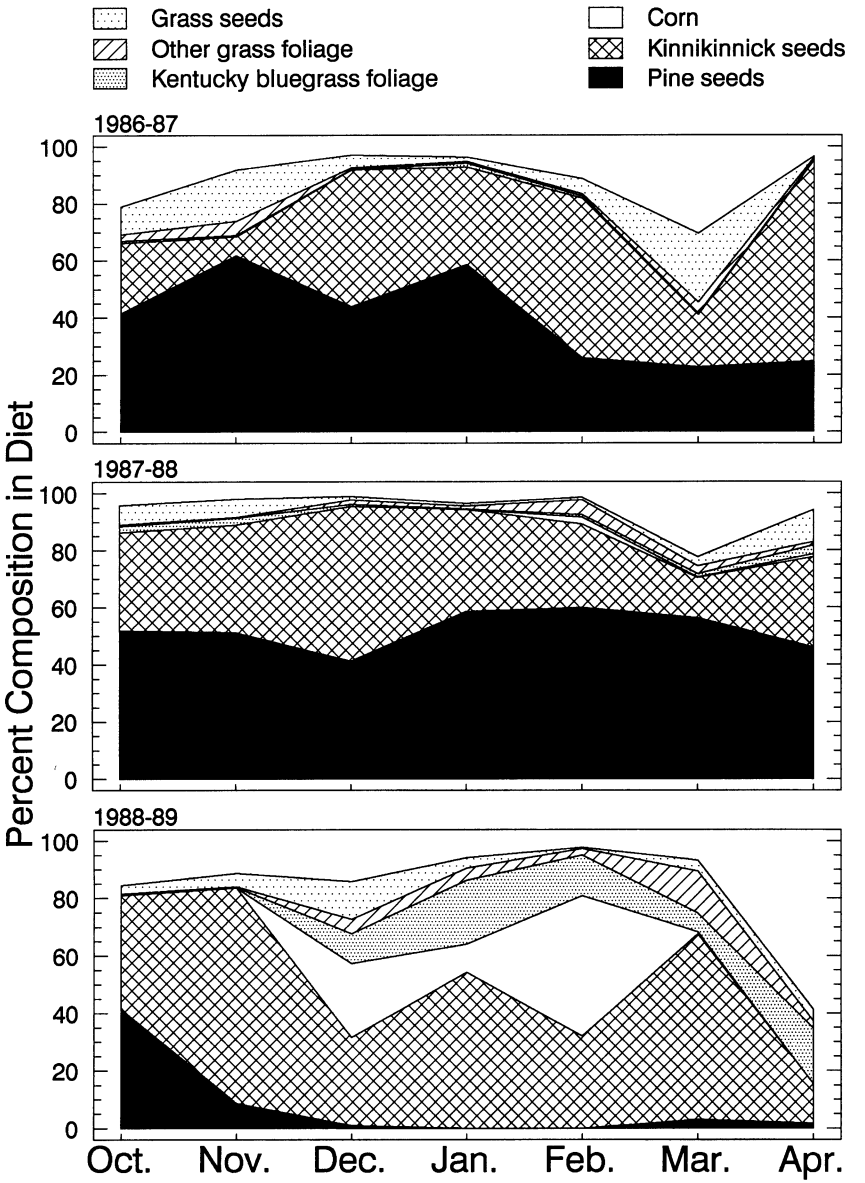

FIG. 3.—Cumulative percent composition of October-April turkey diets 1986–1989

study, averaging 0.6 ± 0.2%, 1.5 ± 0.3% and 9.6 ± 2.7% for 1986–1987, 1987–1988 and 1988–1989, respectively. Turkeys ate more corn ($P \leq 0.01$) during winter 1988–1989 (11.1 ± 4.6%) than during 1986–1987 (0%) and 1987–1988 (0.5 ± 0.4%). Composition of grass seeds in winter turkey diets differed ($P = 0.07$) among years, but no differences were apparent in multiple-range tests. Trends suggest greater consumption of grass seeds during

TABLE 1.—Average understory vegetation production (g/m^2) in major vegetation categories, 1987

	Aspen/birch $\bar{x} \pm SE$		Meadow center $\bar{x} \pm SE$		Meadow edge $\bar{x} \pm SE$		Pine 0–40% OCC $\bar{x} \pm SE$		Pine 41–70% OCC $\bar{x} \pm SE$		Pine >70% OCC $\bar{x} \pm SE$	
Grass	48	11ABC[1]	114	24A	84	18A	55	8AB	23	7B	8	5C
Forbs	51	8A	32	11AB	28	12AB	20	7AB	11	4B	3	2B
Shrubs	38	6A	13	12AB	10	9AB	2	1B	12	7B	3	2B
Total	137	21A	159	26A	122	22AB	77	14AB	46	15BC	14	8C

[1] Within-row averages followed by different letters differed $\alpha = 0.10$, MRPP test among plant communities

1988–1989 (9.1 ± 2.0%) than during 1986–1987 (4.5 ± 4.5%) or 1987–1988 (4.4 ± 0.9%). Grass foliage, other than Kentucky bluegrass, in winter turkey diets did not differ among years.

Food availability.—Understory vegetation in ponderosa pine declined as overstory canopy cover of ponderosa pine increased. Grasses were more ($P \leq 0.03$) abundant in meadows, aspen/birch and ponderosa pine with 0–40% OCC than in ponderosa pine with >40% OCC (Table 1). Forbs and shrubs were most abundant in aspen/birch. Ponderosa pine with >40% OCC had fewer ($P \leq 0.01$) forbs than aspen/birch. Kentucky bluegrass and smooth brome were the most common grass species in our study area.

Pine seed production in 1987 was 10 times greater ($P < 0.01$) than during 1988 (Table 2), but not everywhere as indicated by a significant ($P \leq 0.10$) interaction between years and VEG/OCC. Meadow centers, meadow edges and aspen/birch had fewer ($P \leq 0.10$) pine seeds than ponderosa pine with 41–70% OCC during both years. The production of pine seeds along meadow edges did not differ from other ponderosa pine VEG/OCC categories. Rank correlations between production of ponderosa pine seeds and ponderosa pine basal area were positive (Fig. 4) for both 1987 and 1988 ($r \geq 0.57$, $P \leq 0.01$).

POULT DIETS

Age classes.—Poults 0–3 and 4–7 wk old consumed more ($P \leq 0.05$) beetles (Coleoptera) than poults 8–12 wk old (Table 3). All age classes of poults consumed grasshoppers (Orthoptera) and true bugs (Hemiptera) in similar amounts. Poults 0–3 wk old ate more ants (Hymenoptera) ($P = 0.07$) than poults 4–7 wk old. Total arthropod composition declined ($P = 0.09$) in diets as poults became older. Kentucky bluegrass comprised a greater ($P \leq 0.03$) proportion of diets for poults 0–3 and 4–7 wk old than for older poults. Grass seeds were consumed more ($P \leq 0.09$) by 4–7 and 8–12 wk-old poults than 0–3 wk-old poults. Forb seeds/flowers were consumed more ($P = 0.06$) by poults 8–12 wk of age than poults

TABLE 2.—Average abundance of pine seeds ($seeds/m^2$) in major vegetation categories, 1987–1988

Year	Aspen $\bar{x} \pm SE$		Meadow center $\bar{x} \pm SE$		Meadow edge $\bar{x} \pm SE$		Pine 0–40% OCC $\bar{x} \pm SE$		Pine 41–70% OCC $\bar{x} \pm SE$		Pine >70% OCC $\bar{x} \pm SE$	
1987	3.6	0.7A[1]	1.8	1.1A	10.1	4.5AB	12.0	3.8AB	15.9	2.3B	15.7	4.7AB
1988	<0.1	<0.01A	0.1	0.1A	0.7	0.4AB	1.2	0.4AB	0.9	0.2B	1.1	0.4AB

[1] Within-row averages followed by different letters differed $\alpha = 0.10$ Welch's test among plant communities within years

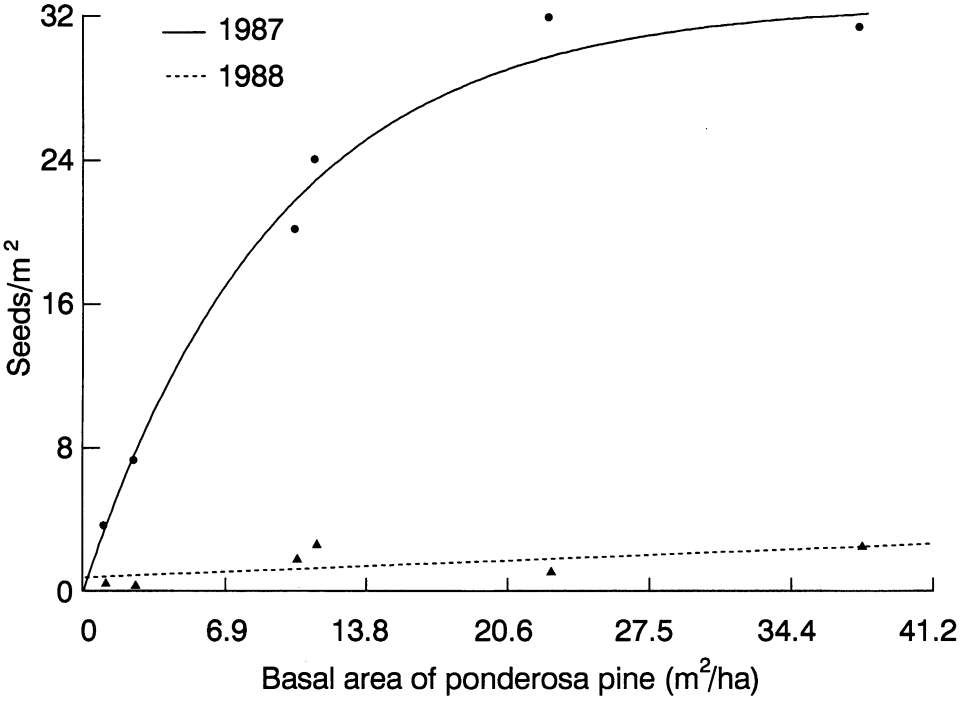

FIG. 4.—Ponderosa pine production (seeds/m²) in relation to ponderosa pine basal area in major vegetation categories 1987–1988. The solid line represents 1987 data and the dashed line represents 1988 data

0–3 wk. Poults 4–7 and 8–12 wk old consumed more ($P \leq 0.03$) soft mast, primarily raspberry (*Rubus idaeus*), than poults 0–3 wk old. Hard mast, primarily kinnikinnick fruits, increased ($P \leq 0.02$) in diets of poults 8–12 wk old compared to poults 0–3 and 4–7 wk old.

Arthropod availability.—More ($P \leq 0.10$) total arthropods occurred in aspen/birch, meadow centers and meadow edges than in ponderosa pine communities (Table 4). For several orders of arthropods, abundance in ponderosa pine 0–40% OCC was intermediate between meadows or aspen/birch communities and ponderosa pine >40% OCC. Ponderosa pine with >40% OCC had fewer arthropods than other VEG/OCC categories. Abundance of arthropods that occurred in poult diets was greater ($P \leq 0.04$) in the meadow centers than other VEG/OCC communities. Aspen/birch and meadow edges had greater ($P \leq 0.05$) abundance of arthropods consumed by poults than ponderosa pine 0–40%. Ponderosa pine 41–70% and >71% OCC had the fewest ($P \leq 0.01$) arthropods that occurred in poult diets. Ranked abundances of arthropods in all orders were correlated with ranked herbaceous biomass among sites ($r \geq 0.6$, $P \leq 0.01$).

Diet selection by poults.—Poults did not select arthropods in proportion to their availability. Rank correlations between biomass of arthropod orders and composition of arthropod orders in diets of poults 0–3 and 4–7 wk old showed no significant relationships ($r \leq 0.49$, $P \geq 0.18$). Poults consumed greater quantities of the large arthropods (Table 5); rank correlation between mass/individual of arthropods and diet composition of poults 0–3 and 4–

TABLE 3.-Percent composition of Merriam's turkey poult diets by age classes 1986-1988

Food types	O-3 wk $\bar{x} \pm$ SE	4-7 wk $\bar{x} \pm$ SE	8-12 wk $\bar{x} \pm$ SE
Coleoptera	29.4 ± 5.4A[1]	24.4 ± 6.1A	7.0 ± 2.5B
Orthoptera	38.8 ± 5.6	48.8 ± 7.2	43.0 ± 8.0
Hemiptera	2.0 ± 1.0	0.1 ± 0.1	0.0 ± 0.0
Hymenoptera	9.2 ± 2.4A	1.5 ± 1.0B	6.0 ± 3.3AB
Other arthropods[2]	2.0 ± 0.8	1.7 ± 1.5	5.1 ± 3.3
Total arthropods	81.4 ± 4.7A	76.5 ± 3.9AB	61.1 ± 9.4B
Bromus spp. foliage	0.9 ± 0.5	0.5 ± 0.3	2.4 ± 1.1
Carex spp. foliage	3.1 ± 0.7	3.0 ± 0.6	1.5 ± 0.5
Kentucky bluegrass foliage	2.3 ± 0.4A	2.0 ± 0.3A	0.7 ± 0.2B
Other grass foliage[2]	1.9 ± 0.8AB	2.4 ± 0.9A	0.5 ± O.lB
Total grass foliage	8.2 ± 1.7	7.9 ± 1.1	5.1 ± 1.2
Grass seeds[2]	5.2 ± 2.7A	5.7 ± 1.5AB	13.4 ± 4.1B
Forb foliage[2]	1.8 ± 0.6	1.1 ± 0.2	0.9 ± 0.4
Forb seeds/flowers[2]	1.4 ± 0.7A	2.0 ± 0.9AB	4.8 ± 1.6B
Soft mast[2]	1.0 ± 0.5	5.8 ± 2.2	4.0 ± 1.7
Hard mast[2]	0.7 ± 0.4	0.9 ± 0.8	10.6 ± 6.0

1 Within-row averages followed by different letters are significantly different $\alpha = 0.10$, MRPP test
2 These food categories include identified and unidentified items

7 wk old were significantly correlated ($r \geq 0.59$, $P \leq 0.09$) in 198'7. In 1988, rank correlations between mass/individual of arthropods and composition in diets of poults were weaker ($r \geq 0.50$, $P \leq 0.12$). The large arthropods did not comprise the greatest biomass of arthropods available to poults. Rank correlations between mass/individual and biomass of arthropods showed nonsignificant negative correlations ($r \geq -0.2$, $P \geq 0.61$). Grasshoppers were more ($P < 0.01$) abundant during 1988 than 1987 and comprised a greater ($P < 0.01$) proportion of poult diets in 1988. Concomitant with increased consumption of grasshoppers, was a decrease ($r \leq -0.3$, $P \leq 0.08$) in dietary composition of arthropod orders of lower ranked mass/individual.

DISCUSSION

ADULTS

Adult Merriam's turkeys consumed many different kinds of foods. When diets were evaluated for the study period as a whole, Merriam's turkeys appeared to feed without regard to availability. However, foods consumed by turkeys showed temporal and spatial variation that reflected the unavailability of apparently preferred foods. Animals cannot select resources that may be spatially or temporally unavailable. Contrary to Hurst (1992), we do not believe Merriam's turkeys were opportunistic foragers.

Summer diets.-Summer diets of Merriam's turkeys in the Black Hills included more food items than winter diets. During summer, turkeys mostly consumed grass seeds. Despite being abundant, grass foliage was a minor component in turkey diets, during our study and that of Petersen and Richardson (1975). However, grass foliage was prominent in diets of Merriam's turkey from Montana, Arizona and New Mexico (Jonas, 1966; Scott and Boeker, 1973; Schemnitz ***et al.,*** 1985). Grass seeds were important summer turkey foods in Wyoming (Hengel, 1990). The lack of grass seeds in turkey diets on the Fort Apache Indian

TABLE 4.—Average number of arthropods in 45 passes of a sweep net in major vegetation categories, 1987–1988[1]

Orders	Aspen $\bar{x} \pm SE$	Meadow center $\bar{x} \pm SE$	Meadow edge $\bar{x} \pm SE$	Pine 0–40% OCC $\bar{x} \pm SE$	Pine 41–70% OCC $\bar{x} \pm SE$	Pine >70% OCC $\bar{x} \pm SE$
Araneida	8.1 ± 0.8A[2]	5.3 ± 1.1AB	5.0 ± 1.1AB	2.8 ± 0.6BC	2.2 ± 0.4C	2.0 ± 0.5BC
Coleoptera	18.2 ± 2.5A	24.7 ± 7.8AB	12.0 ± 3.6A	6.3 ± 1.3B	3.2 ± 0.7C	0.9 ± 0.6C
Diptera	26.0 ± 2.4A	43.2 ± 9.7A	38.3 ± 13.1A	11.7 ± 2.1B	8.9 ± 1.2B	5.9 ± 1.4B
Homoptera	85.7 ± 20.3A	146.6 ± 30.8AB	67.6 ± 19.8B	28.0 ± 4.8AC	18.3 ± 3.9C	6.6 ± 2.3C
Hemiptera	15.9 ± 1.9A	41.9 ± 8.1A	12.6 ± 2.7B	8.0 ± 1.9A	1.9 ± 0.5C	1.0 ± 0.6C
Hymenoptera	36.1 ± 2.8A	20.3 ± 3.4B	17.7 ± 3.6B	5.5 ± 0.8C	5.2 ± 1.1CD	1.8 ± 0.6D
Orthoptera	0.6 ± 0.2AC	5.8 ± 1.2B	2.8 ± 0.7B	0.8 ± 0.2A	0.4 ± 0.1C	0.0 ± 0.0C
Total[3]	195.5 ± 23.3A	291.9 ± 45.2A	163.6 ± 29.5A	64.6 ± 8.5B	43.6 ± 6.9C	19.0 ± 4.1C
Consumed[4]	78.9 ± 5.1A	97.9 ± 13.3B	51.3 ± 8.5A	23.4 ± 3.4C	12.9 ± 2.0D	5.9 ± 1.6D

[1] Average biomass of arthropods can be estimated from average weight per individual in Table 5

[2] Within-row averages followed by different letters are significantly different at $\alpha = 0.10$, MRPP test

[3] Includes all arthropods collected

[4] Average number of arthropods that occurred in turkey poult diets

TABLE 5.-Mass/individual of arthropod orders from sweep net samples collected from meadows 1987-1988

Order	Average mass (g)	
	1987	1988
Homoptera	0.0011	0.0009
Hemiptera	0.0027	0.0026
Hymenoptera	0.0021	0.0011
Lepidoptera	0.0125	0.0119
Diptera	0.0011	0.0013
Orthoptera	0.0373	0.0432
Coleoptera	0.0031	0.0036
Arachnida	0.0025	0.0029
Collembola	0.0008	0.0007

vation, Arizona, was attributed to overgrazing by livestock (Scott and Boeker, 1973). Forbs were minor components in Black Hills turkey diets and soft mast was consumed only as berries ripened in late June and July.

Spring 1988 was the beginning of a severe drought in the Black Hills. Temperatures were higher than average (South Dakota Climatological Summary, 19861988, U.S. Dep. Comm., Asheville, N.C.) and herbaceous production was low (Rumble, 1990). Seeds from smooth brome were absent from turkey diets after July. Turkeys consumed more soft mast, possibly to meet water requirements. Consumption of arthropods by adult turkeys was likely related to scarcity of grass seeds rather than to abundance of arthropods. Consumption of grasshoppers was disproportionate to changes in their abundance between 1988 and 1987. In 1988, adult turkeys consumed five times more grasshoppers than in 1986 when grasshoppers were more abundant than in any other year of our study (MAR, pers. observ.). Turkeys' diets showed temporal variation, but spatial variation in summer microhabitats was not evident (Rumble and Anderson, 1996).

Winter diets.-Ponderosa pine seeds were the preferred winter food of the turkeys we studied and turkeys in Montana (Jonas, 1966) and Arizona (Scott and Boeker, 1973). More recently, Wakeling and Roger (in press) found a lower proportion of ponderosa pine seeds in turkey diets than occurred at feeding sites, but they did not correct for underestimation bias of ponderosa pine seed in diets determined from fecal samples (e.g., Rumble and Anderson, 1993a). The turkeys we studied consumed more ponderosa pine seeds in years of higher availability, switching to kinnikinnick fruits during late winter and in years when pine seeds were unavailable. Kinnikinnick fruits contain 19% less energy than ponderosa pine seeds (Rumble, 1990).

The importance of ponderosa pine seeds in diets of Merriam's turkeys is limited by their availability (Korschgen, 1967). Seed crops of ponderosa pine are sporadic (Oliver and Ryker, 1990) over most ranges of Merriam's turkeys, but occur regularly in the Black Hills (Boldt and Van Duesen, 1974). Above average precipitation during 1986 and 1987 resulted in ready availability of ponderosa pine seeds. Pine seeds comprised 40% and 52% of turkey diets during the subsequent winters, respectively, and turkeys selected microhabitats with basal area near the maximum for pine seed availability. Ponderosa pine seeds were four times more abundant at turkey microhabitats than they were on average in ponderosa pine communities (Rumble and Anderson, 1996). Merriam's turkeys in Arizona selected feeding sites with greater abundance of ponderosa pine seeds than at random (Wakeling and Rog-

ers, in press). Following drought and failure of the pine crop in 1988, turkey diets varied temporally and this was reflected in spatial variation in habitat selection patterns. Turkey diets during the following winter were mostly kinnikinnick fruits, grass foliage and grass seeds. Ponderosa pine seed was a minor food in turkey diets after December. Turkeys consequently selected habitats that winter with lower basal area (Rumble and Anderson, in press) and more understory vegetation (Uresk and Severson, 1989) than in previous years Kentucky bluegrass was abundant in our study, but was consumed more during winter 1988-1989 than in previous years. Corn was available every winter at trap/bait stations, private residences and ranches; it was mostly ignored except following snow storms and during 1988-1989.

Protein requirements of turkeys increase during nesting, and new growth green vegetation provides a source of high protein (Robbins, 1983). Turkeys consumed increasing amounts of foliage and arthropods during early spring with the approaching breeding season. Turkeys increasingly selected habitats with open canopies containing understory vegetation during spring (Rumble and Anderson, in press).

POULTS

Turkey poults require 28% dietary protein (National Research Council, 1977) that they obtain from arthropods (see Hurst, 1992, for review) for muscle and feather development (Robbins, 1983). Dietary protein requirements of poults decrease and energy requirements increase after 8 wk (National Research Council, 1977) corresponding with completion of feather development (Leopold, 1943). Merriam's turkey poults in the Black Hills consumed diets high in arthropods through 7 wk of age. Some studies noted declines in consumption of arthropods by eastern turkey poults *(Meleagris gallopavo silvestris)* >4 wk of age (Hurst, 1992). Despite increased consumption of vegetation by poults >7 wk old, arthropods still comprised >60% of all poult diets in our study.

Diet selection by poults-Total arthropods were most abundant in meadows, which were the most commonly selected macrohabitat by hens with poults (Rumble and Anderson, 1993b). Of the arthropods consumed by poults, grasshoppers and beetles had the greatest mass/individual and comprised the greatest proportion of diets. Only Hemiptera abundance differed between meadow centers and meadow edges, but they comprised only a small proportion of poult diets. If arthropod abundance from meadow edges and meadow centers are compared, grasshoppers and arthropods that occurred in poult diets were more abundant in meadow centers (Rumble, 1990). Hens with poults predominantly selected meadow edges and were seldom observed more than 5 m from the forest edge (Rumble, 1990). Greater exposure to predators in meadow centers could cause hens with poults to select meadow edges over meadow centers. Predator avoidance has been shown to constrain selection of foraging habitats of white-throated sparrows *(Zonotrichia albicollis)* (Schneider, 1984) and may be why Sharp-tailed grouse *(Tympanuchus phasianellus)* in Nebraska did not select habitats with the greatest abundance of invertebrates (Kobridger, 1965). Intensive sampling of foods, food availability and microhabitats of hens with poults is needed to complete our understanding of constraints on foraging site selection by hens with poults.

Poults selectively consumed arthropods available to them. Proportions of arthropods in diets of poults ≤7 wk old could not be attributed to available biomass of arthropods. Poults ate more of the large mass/individual arthropods, but orders of large arthropods did not comprise greater biomass available to poults. Poults did not eat arthropods smaller than ants. The mass/individual of leafhoppers was lower than for ants and they were the most abundant arthropod. However, leafhoppers were not eaten by poults in our study nor by poults in Wyoming (Hengel, 1990). Leafhoppers were common foods of eastern turkey

poults (Hurst and Stringer, 1975; Healy, 1985). Arthropods with lower mass/individual than grasshoppers constituted a greater proportion of poult diets when grasshoppers, which had the greatest mass/individual, were less abundant. Diets and feeding rates of savannah sparrows *(Passerculus sandwichenis)* also have been shown to vary with grasshopper abundance (Miller *et al.,* 1994).

Acknowledpents. - The U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station; National Wild Turkey Federation; and South Dakota Game, Fish and Parks provided financial support for this research. Dr. A. J. Bjugstad (deceased) provided initial advice and encouragement. T. R. Mills, C. D. Oswald, K. J. Thorstenson, K. L. Jacobson, L. J. Harris and R. A. Hodorff provided technical assistance. M. P. Green was a volunteer throughout this study and R. L. Taylor allowed access to his property. M. Morrison, J. G. MacCracken, H. G. Shaw, L. D. Flake and B. F. Wakeling reviewed drafts of this manuscript.

LITERATURE CITED

BOLDT, C. E. AND J. L. VAN DUESEN. 1974. Silviculture of ponderosa pine in the Black Hills: the status of our knowledge. U.S. *For. Serv. For. Range Exp. Stn. Res. Pap. RM-124.* Fort Collins, Colo. 45 p.

BROWN, M. B. AND A. B. FORSYTHE. 1974. Robust test for equality of variances. *J. Am. Stat. Assoc., 69: 364-367.*

DAUBENMIRE, R. D. 1959. A canopy-coverage method of vegetational analysis. *Northwest Sci., 33:43-64.*

DICKMAN, C. R. AND C. HUANG. 1988. The reliability of fecal analysis as a method for determining the diet of insectivorous mammals. *J. Mammal., 69: 108-113.*

DIXON, W. J. AND F. J. MASSER, JR. 1969. Introduction to statistical analysis. McGraw-Hill, Inc., New York. 638 p.

DUNNETT, C. W. 1980. Pairwise multiple comparisons in the unequal variance case. *J. Am. Stat. Assoc., 75:796-800.*

GREAT PLAINS FLORA ASSOCIATION. 1986. Flora of the Great Plains. R. L. McGregor, coord. Univ. Kansas Press, Lawrence. 1392 p.

GRIFFING, J. P. 1985. The spherical densiometer revisited. Southwest habitater Vol. 6, No. 2, U.S. For. Serv., Reg. 3. Albuquerque, N.M. 2 p.

GULLION, G. W. 1966. A viewpoint concerning the significance of studies of game bird food habits. *Condor; 68:372-376.*

HAVSTAD, K. M. AND G. B. DONART. 1978. The microhistological technique: testing two central assumptions in south-central New Mexico. *J. Range Manage.,* 31:469-470.

HEALY, W. M. 1985. Turkey poult feeding activity, invertebrate abundance, and vegetation structure. *J. Wildl. Manage., 49:466-472.*

HENGEL, D. A. 1990. Habitat use, diet and reproduction of Merriam's turkeys near Laramie Peak, Wyoming. M.S. Thesis, Univ. Wyoming, Laramie. 220 p.

HUMPHREY, D. L. 1985. Use of biomass predicted by regression from cover estimates to compare vegetational similarity of sagebrush-grass sites. *Great Basin Nat., 45:94-98.*

HURST, G. A. 1992. Foods and feeding, p. 6683. *In:* J. G. Dickson (ed.). The wild turkey, biology and management. Stackpole Books. Harrisburg, Pa.

---------AND B. D. STRINGER. 1975. Food habits of wild turkey poults in Mississippi. *Proc. Nat. Wild Turkey Symp., 3:76-86.*

——— AND W. E. POE. 1985. Amino acid levels and patterns in wild turkey poults and their food items in Mississippi. *Proc. Nat. Wild Turkey Symp., 5:133-143.*

JONAS, R. 1966. Merriam's turkeys in southeastern Montana. *Mont. Game Fish Dep. Tech. Bull. No. 3,* Helena. 36 p.

KOBRIDGER, G. D. 1965. Status, movements, habitats and foods of prairie grouse on a sandhills refuge. J. *Wildl. Manage.,* 29:788-800.

KORSCHGEN, L. J. 1967. Feeding habits and foods, p. 137-198. *In: 0.* H. Hewitt (ed.). The wild turkey and its management. Wildl. Washington, D.C.

LAUDENSLAGER, S. L. AND L. D. FLAKE. 1987. Fall food habits of wild turkeys in south central South Dakota. *Prairie Nat., 19:37-40.*

LEMMON, P. E. 1956. A spherical densiometer for estimating forest overstory density. *For. Sci.,* 2:314-320.

LEOPOLD, A. S. 1943. The molts of young wild and domestic turkeys. Condor, 45:133-145.

LEWIS, S. W. 1994. Fecal and rumem analysis in relation to temporal variation in black-tailed deer diets. *J. Wildl. Manage., 58:53-58.*

MARTI, C. 1982. Accuracy of fecal analysis for identifying foods of black grouse. *J. Wildl. Manage., 46:* 773-777.

MIELKE, P. W. 1984. Meteorological applications of permutation techniques based on distance functions. *Hundb. Stat., 4:813-830.*

MILLER, C. K., R. L. KNIGHT, L. C. MCEWEN AND T. L. GEORGE. 1994. Responses of nesting savannah sparrows to fluctuations in grasshopper densities in interior Alaska. *Auk, 111:962-969.*

MILLIKEN, G. A. AND D. E. JOHNSON. 1984. Analysis of Messy Data Volume 1: Designed experiments. Van Nostrand Reinhold Co., New York. 473 p.

NATIONAL RESEARCH COUNCIL. 1977. Nutrient requirements of domestic animals: nutrient requirements of poultry. Natl. Acad. Sci., Wash., DC. 62 p.

OLIVER, W. W. AND R. A. RYKER. 1990. Pinus ponderosa; p. 413-424. *In:* R. M. Burns and B. H. Honkla (tech. coords) . Silvics of North America: Vol. 1, Conifers. *Agroc/ Hundb. 654.* U.S. For. Serv., Washington, D.C.

ORR, H. K. 1959. Precipitation and stream flows in the Black Hills. U.S. *For. Serv. Stn. Pap.* RM-44. Rocky Mtn. For. Range Exp. Stn., Fort Collins, Colo. 25 p.

PAYNE, G. F. 1974. Cover-weight relationships. J. *Range Manage., 27:403-404.*

PETERSEN, L. E. AND A. H. RICHARDSON . 1975. The wild turkey in the Black Hills. South Dakota Dep. Game Fish and Parks. Bull. No. 6. Pierre. 51 p.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, Inc., New York. 343 p.

RUMBLE, M. A. 1990. Ecology of Merriam's turkeys *(Meleagris gallopavo merriani)* in the Black Hills, South Dakota. Ph.D. Dissertation. Univ. Wyoming, Laramie. 169 p.

------AND S. H. ANDERSON. 1992. Stratification of habitats for identifying habitat selection by Merriam's turkeys. *Great Basin Nat., 52:* 139-l 44.

-------AND -------1993a. Evaluating the microscopic fecal technique for estimating hard mast in turkey diets. U. S. *For. Serv.,* Res. *Pap.* RM-3 10. Rocky Mtn. For. Range Exp. Stn., Fort Collins, Colo. 4 p.

- - - - A N D —— 1993b. Habitat selection of Merriam's turkey *(Meleagris gallopano merriami)* hens with poults in the Black Hills, South Dakota. *Great Basin Nat., 53:131-136.*

- - - - A N D —— 1996. Microhabitats of Merriam's wild turkeys in the Black Hills, South Dakota. *Ecol. Appl., 1:226-334.*

SCHEMNITZ, S. D., D. L. GOERNDT AND K. H. JONES. 1985. Habitat needs and management of Merriam's turkeys in southcentral New Mexico. *Proc. Natl. Wild Turkey Symp.,* 5:199-232.

SCHNEIDER, K. J. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. *Ecology, 65: 1820-l 827.*

SCOTT, V. E. AND E. L. BOEKER. 1973. Seasonal food habits of Merriam's turkeys on the Fort Apache Indian Reservation, p. 151-158. *In: G. C.* Sanderson and H. C. Schultz (eds.). Wild turkey management: current problems and programs. MO. Chap. Wildl. Soc. and Univ. MO. Press, Columbia.

SHARPE, G. W., C. W. HENDEE AND S. W. ALLEN . 1976. Introduction to Forestry. McGraw-Hill Book Co. 544 p.

SPARKS, D. R. AND J. C. MALACHEK. 1968. Estimating percentage dry weights in diets using a microscopic technique. *J. Range Manage., 21:264-265.*

URESK, D. W. AND K. E. SEVERSON. 1989. Understory-overstory relationships in ponderosa pine forests, Black Hills, South Dakota. J. *Range Manage., 42:203-208.*

WAKELING, B. F. AND T. D. ROGERS. 1996. Winter diet and habitat selection by Merriam's turkeys in northcentral Arizona. *Proc. Natl. Wild Turkey* In press.

SUBMITTED 3 JULY 1995 ACCEPTED 14 FEBRUARY 1996