

SEX DIFFERENCES IN QUALITY OF WHITE-TAILED DEER DIETS

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ABSTRACT.—This study tested the hypothesis that female white-tailed deer (*Odocoileus virginianus*) select a higher quality diet than males, as suggested by McCullough's (1979) evidence for resource partitioning between the sexes. Fecal samples from 136 adult female and 95 adult male deer were collected during 1982–83 on the E. S. George Reserve, Michigan. These fecal samples, and rumen and fecal samples from deer shot in winter 1980–81, were analyzed for winter diet composition by forage class, and for year-long diet quality as indexed by fecal nitrogen (FN). Year-round, females had significantly higher FN levels than males. In winter, females consumed significantly more grass and less browse than males. Thus, females consumed diets of higher quality than did males.

Darwin (1871) suggested that the sexes may differ ecologically and thereby reduce intraspecific competition. Niche differences between sexes in birds have received considerable attention (Selander, 1972). Although sexual segregation outside of rut is well known among ungulates (Darling, 1937; Hirth, 1977; Murie, 1951; Welles and Welles, 1961), only recently has attention been given to differences in food habits between the sexes (McCullough, 1985; Shank, 1982; Takatsuki, 1980; Warren and Krysl, 1983). In particular, several authors noted a tendency for female cervids to occupy better habitat than males (Bowyer, 1984; Jackes, 1973; Watson and Staines, 1978) or to consume more nutritious forage (Staines and Crisp, 1978; Staines et al., 1982).

McCullough (1979) showed that the recruitment rate of white-tailed deer (*Odocoileus virginianus*) on the George Reserve, Michigan was negatively correlated with the number of adult females ($r^2 = 0.62$), and independent of the number of males ($r^2 = 0.06$). He suggested that differential use of resources by sex might account for this apparent lack of competition between the sexes. I investigated the George Reserve deer population to test the hypothesis that adult female white-tailed deer consume a higher quality diet than males.

STUDY AREA

The Edwin S. George Reserve, Livingston County, Michigan, USA (42°30'N, 84°W) is a 464-ha natural area owned by the University of Michigan. The land is rugged, morainic old farmland that was abandoned by 1926. It contains wooded hills and knobs, numerous wetlands, and a long esker ridge. The Reserve is 25% grassland, 47% hardwood forests, 13% tamarack (*Larix laricina*) swamps, 8% freshwater marsh, with the remaining 7% divided among ecotones, leatherleaf (*Chamaedaphne calyculata*) bogs, and open water (Roller, 1974). Vegetation types are interspersed in a fine-grained pattern such that a variety of vegetation types are present in any individual deer's home range (McCullough, 1979).

Approximately 250 deer were present on the reserve in mid-1980, of which 85 were harvested during winter 1980–81. Of the approximately 160 deer present in mid-1982, eight adults of each sex were marked with distinctive collars. Thirty-five deer were harvested during autumn 1982. A detailed history of the herd is given by McCullough (1979).

METHODS

Point-frame analysis (Chamrad and Box, 1964) was performed on rumen content samples collected from 8 male and 20 female deer shot during 10 January–8 February 1981. Samples from this month were chosen because it was the only recent period during which males and females were harvested simultaneously, allowing between-sex comparisons without the confounding effect of seasonal differences. Rumen contents were mixed, a large handful was pressed in cheesecloth to remove rumen liquor, and samples were stored frozen until analyzed. For each sample, a portion of the rumen contents was thawed and spread in a 1-cm thick layer in a laboratory tray. Thin layers of material were avoided to reduce biases due to larger leaf blades occupying a large area despite having low volume (McCullough, 1985). From each sample, 100

random points were recorded as oak (*Quercus*) mast, juniper (*Juniperus communis* or *J. virginianus*) berry, mushroom, other fruit or seed, forb, grass or grass-like, oak browse, juniper browse, other browse, or unidentifiable. When the point fell on an unidentifiable item, the nearest identifiable fragment to the point was recorded so that the combination of direct hits and nearest identifiable fragments totalled 100. The results of analyses counting direct hits were virtually identical to the results counting the nearest identifiable fragments (chi-square test for homogeneity, $\chi^2 = 2.62$, 8 d.f., $P = 0.956$). Therefore, results from the two techniques were pooled for analysis of diet differences between sexes. The chi-square test can yield unreliable results when the expected frequency in any cell is <5 . Therefore, results for juniper berries and acorns were pooled with data for unidentified fruit or seed, and forbs were lumped with grasses, before testing for differences between sexes.

Coblentz (1970) and McCullough (1985) reported that winter diets of George Reserve deer were influenced strongly by snow cover; high consumption of browse occurred at snow depths >7.6 cm, but higher grass consumption was observed at lesser snow depths. Therefore, chi-square tests were performed to examine sex differences in diet under conditions of snow cover versus snow absence (defined as snow depth <7.6 cm), as well as for diet differences between sexes over all dates.

Fecal nitrogen (FN) was used as an index of diet quality. For cervids and bovids, FN has shown strong and positive correlations with dietary protein (Erasmus et al., 1978; Hinnant, 1979; Holechek et al., 1981; Jarrige, 1965; Mould and Robbins, 1981; Robbins, 1983), diet digestibility (Holechek et al., 1981; Holloway et al., 1981; Jarrige, 1965; Scales et al., 1974; Wallace and Van Dyne, 1970), and gross energy intake (Holloway et al., 1981).

Whereas most studies using the FN index have used domestic or penned animals fed controlled diets, several also supported the utility of FN in studies of free-ranging ungulates. High concentrations of phenolic compounds in natural diets can render proteins undigestible (Mould and Robbins, 1981). Nonetheless, Leslie and Starkey (1985) reported that FN was significantly correlated with both dietary protein and with diet digestibility in free-ranging populations of elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*). This strong relationship held despite seasonal diets for both species that were high in phenolic compounds. Leslie and Starkey (1985) suggested that the protein-binding effect of phenolics may be mitigated in the complex rations chosen by cervids. Similarly, Gates and Hudson (1979) reported that fecal nitrogen was a good indicator of weight gain in elk feeding freely on complex natural diets, and Holechek et al. (1982) showed that FN predicted average daily weight gain and dietary nitrogen for free-ranging cattle.

Differences in FN might reflect sex differences in digestion rather than diet. However, Thompson et al. (1973) reported that, for a given level of protein intake, male white-tailed deer in feeding trials exhibited identical or trivially higher FN concentrations than females.

From 1 August 1982 through 31 July 1983, fecal samples were collected whenever adult or yearling animals of known sex were observed to defecate. During seasons when antlers were not present, I observed unmarked animals with 7 by 35 binoculars or 20 by 70 spotting scope until external genitalia, or the presence or absence of pedicels, could be seen. I attempted to collect no more than one sample from an individual deer within a sampling period. Frozen fecal samples from animals shot in November 1980 and January 1981 also were used; the January 1981 samples correspond to the rumen samples used to examine forage classes consumed by deer. Samples were dried in a forced-air oven at 60°C for 48 h, ground in a Wiley mill with a 20-mesh screen, and stored in air-tight vials for later analysis.

Because season of collection was expected to affect diet quality, relatively short sampling periods (1 month) were planned within which between-sex comparisons could be made. August–September 1982 samples, however, were pooled into one sampling period, and the January–March 1983 samples were regrouped into 2 6-week periods, so that each sampling period contained a minimum of 7 samples per sex. This is one more than the minimum number of rumen samples needed by Staines et al. (1982) to establish nitrogen differences between sexes of red deer (*Cervus elaphus*).

A 1-g portion of each fecal sample was analyzed for nitrogen using the macro-Kjeldahl method (Horwitz, 1975). Within each period the null hypothesis that male and female FN levels were equal was tested using one-way analysis of variance (ANOVA) with date of collection as a covariate to remove the influence of collection date within sampling period. Within each period, an F -test supported ($P < 0.05$) the assumption that variances for males and females were equal. The Bartlett-Box test for homogeneity (Nie, 1983) indicated that variances across sampling periods were heterogeneous ($F = 4.74$, $P < 0.001$). Therefore, the Wilcoxon signed-ranks statistic (Sokal and Rohlf, 1981) was used to test for sex differences over all 12 periods. Differences in FN between consecutive sampling periods (sexes combined) in 1982–83 were evaluated with t -tests; separate variance estimates were used in t -tests when variances between pairs were significantly different (F -test, $P < 0.05$).

For the one period in which data on FN and diet composition were available (January 1981), linear

TABLE 1.—*Botanical composition of diets of yearling and older white-tailed deer, for samples collected 10 January to 8 February 1981 at the George Reserve, Michigan. The last three columns show the correlation of each forage type (sexes combined) with fecal nitrogen (FN).*

Forage type	Percent of diet		Correlation with FN		
	Males (n = 8)	Females (n = 20)	r	r ²	P
Acorns	0.0	0.1	a		
Juniper berries	0.7	1.3	+0.28	0.08	0.16
Mushrooms	0.8	0.9	-0.26	0.07	0.19
Other fruit/seed	2.6	2.2	+0.08	0.01	0.82
Total fruit and seed	4.1	4.5	+0.05	0.002	0.82
Forbs	0.0	0.3	a		
Grass	6.1	15.0	+0.53	0.28	0.005
Total forb and grass	6.1	15.3	+0.54	0.29	0.004
Oak browse	6.8	11.4	-0.08	0.01	0.70
Juniper browse	47.1	45.7	-0.05	0.002	0.81
Other browse	35.9	23.1	-0.25	0.06	0.22
Total browse	89.9	80.2	-0.45	0.20	0.022

* Indicates r not computed due to this food being present in <5 samples.

correlations were used to examine relationships between FN and forage types. Because the forage variables were expressed as percents, these data were arcsine-square-root transformed before calculating correlation coefficients (Sokal and Rohlf, 1981).

RESULTS

Sex differences in forage classes.—Although both sexes were primarily browsers in winter, females used more grass and less browse than did males (Table 1); the difference between sexes in food habits was significant ($\chi^2 = 90.8$, 5 *d.f.*, $P < 0.005$). Differences between male and female diets were consistent and significant both for collection dates when snow cover was present ($\chi^2 = 63.4$, 5 *d.f.*, $P < 0.05$, 6 males, 12 females) and for snow-free collection dates ($\chi^2 = 22.9$, 5 *d.f.*, $P < 0.05$, 2 males, 8 females).

Sex differences in fecal nitrogen.—Fecal nitrogen was determined for 165 fecal samples from female deer and 117 samples from male deer over the 10 sampling periods in 1982–83 and the 2 sampling periods in 1980–81. Variation among periods was highly significant (two-way ANOVA, $F = 147$, 11 *d.f.*, $P < 0.001$). Comparison of within-period averages adjusted for collection date showed that females had consistently higher FN concentration than males (Table 2). Although the difference between sexes was significant ($P < 0.05$) in only 4 of 12 sampling periods (Table 2), the Wilcoxon signed-ranks test indicated that throughout the year females displayed significantly higher FN concentrations than did males ($T = 4.5$, $n = 12$, $P < 0.005$).

Differences in FN between consecutive sampling periods were significant for all pairwise contrasts ($P < 0.001$ for all pairs except February–March vs. April, $P = 0.008$; May vs. June, $P = 0.001$; and October vs. November, $P = 0.038$). Within each period except March, October, and November 1982, FN showed a significant linear trend with date of collection (significance of the covariate day in ANOVA of FN by sex, $P < 0.05$).

The FN difference between sexes in January 1981 was evident both on days with snow cover (means \pm SE: 13 females, $1.69 \pm 0.05\%$; 6 males, $1.50 \pm 0.07\%$; one-way ANOVA, $F = 3.88$, $P = 0.066$) and without snow cover (8 females: $1.87 \pm 0.06\%$; 2 males: $1.56 \pm 0.07\%$; $F = 5.67$, $P = 0.044$). No sampling dates during 1982–83 had snow cover > 7.6 cm.

Of all components of the winter diet, percent grass had the strongest positive correlation with FN ($r = +0.53$, $n = 28$, $P = 0.005$) (Table 1). Individual browse components were negatively but nonsignificantly correlated with FN; the sum of all browse components had a significant negative correlation with FN ($r = -0.45$, $P = 0.022$).

Animal age, weight, and length data for the January 1981 samples were used to examine effects of animal age and size on FN. No correlation occurred between FN and body weight

TABLE 2.—Average fecal nitrogen concentration (FN, percent), adjusted for date of collection within period, by sex and sampling period for yearling and older white-tailed deer at the George Reserve, Michigan. Ratio is that of male mean to female mean. P determined by one-way ANOVA of FN by sex with collection date as a covariate.

Sampling period	Males		Females		Ratio	P
	Mean (SE)	n	Mean (SE)	n		
Nov 1980	2.15 (0.08)	14	2.23 (0.11)	9	0.96	0.58
Jan 1981	1.51 (0.05)	8	1.75 (0.05)	21	0.86	0.006
Aug–Sep 1982	2.70 (0.06)	11	2.74 (0.06)	11	0.99	0.70
Oct 1982	1.95 (0.08)	8	1.97 (0.11)	14	0.99	0.96
Nov 1982	2.07 (0.03)	8	2.12 (0.05)	12	0.98	0.50
Dec 1982	1.68 (0.03)	7	1.84 (0.03)	11	0.91	0.002
1 Jan–14 Feb 1983	1.53 (0.05)	9	1.59 (0.03)	15	0.96	0.32
15 Feb–31 Mar 1983	1.85 (0.06)	10	1.83 (0.04)	11	1.01	0.82
Apr 1983	1.92 (0.07)	13	2.08 (0.04)	17	0.92	0.04
May 1983	3.35 (0.09)	12	3.46 (0.08)	21	0.97	0.42
Jun 1983	3.81 (0.09)	8	3.80 (0.04)	14	1.00	0.92
Jul 1983	3.13 (0.07)	8	3.34 (0.07)	11	0.94	0.01

($r = +0.02$, $n = 28$, $P = 0.92$), or between FN and body length ($r = +0.07$, $P = 0.76$). Similarly, age class (6 yearlings, 14 2-year-olds, 6 >2-year-old deer) had no effect on FN (one-way ANOVA, $F = 0.458$, $P = 0.80$).

DISCUSSION

Sex differences in diet.—In January 1981, females consumed more grass and less browse than males. This difference underlies part of the between-sex difference in FN, and was most pronounced on snow-free collection dates, when grasses were most available (McCullough, 1985). The differences in grass and browse consumption noted herein are consistent with the observed differences in FN, and support the prediction that females consume higher quality diets.

Due to bias in sampling design (buck harvest preceding doe harvest by several weeks), very few studies have been able to contrast diets by sex. Only three other studies on white-tailed deer report significant differences in diets between sexes. Warren and Krysl (1983) noted that males in Texas ate more acorns and oak browse than did females. McCullough (1985) reported that autumn–winter acorn consumption by 2- and 3-year-old females was lower than for other-aged females and males. Further, lowered consumption of acorns was associated with higher consumption of other fruits and seeds. Korschgen et al. (1980) compared the sexes in spring–summer consumption of 26 food species in Missouri and found only two nominally significant differences: males ate more summer grape (*Vitis aestivalis*) and more Korean lespedeza (*Lespedeza stipulacea*).

Sex differences in fecal nitrogen.—The highly significant changes in FN across sampling periods, and the significant linear trends of FN with collection day within sampling period, indicate that FN is a sensitive index of seasonal diet changes. Further, these changes closely reflect the pattern of food habits of George Reserve deer as independently determined by McCullough (1985), and the quality of those foods as reported by McCullough and Ullrey (1985). The rapid increase in FN in spring corresponded to consumption of the nutritious new growth of grasses and forbs. FN then slowly declined during summer and autumn as diets shifted to maturing browse. The low FN in autumn, along with the high variance in FN, coincided with availability of acorns and fruits and with the age-sex differences in mast consumption. The lowest FN levels occurred in winter when deer fed on the lowest quality foods; FN increased significantly during snow-free periods when grasses were available.

In addition to the seasonal trend, FN levels were higher in females than males. The largest differences were evident in December and January. During these months, little high quality food is available, and resource partitioning would be advantageous. However, such partitioning may be even more advantageous later in winter, when metabolic needs are increasing but forage quality remains low.

Robbins (in litt.) reported that the relationship between FN and dietary nitrogen and diet digestibility also is affected by the type of forage consumed. Robbins' data show that the protein in grass may make a smaller contribution to FN than a similar quantity of protein in winter browse. Thus, the FN difference observed herein for winter probably underestimates the sex difference in winter diet quality, because females consumed more grass and less woody browse than did males.

Sex differences in feeding behavior.—Adult female deer on the George Reserve consistently selected a higher quality diet than did adult males. These differences in diet may reflect 1) spatial overlap between sexes but differences in selection of forage species or plant parts, or 2) spatial separation of sexes so that they forage in areas with different feeding opportunities.

Most explanations involving spatial overlap but separate diets consider the feeding difference to be a result of allometric relationships between body size, digestive capacity, and metabolic requirements. An adult (>2.5 years old) male white-tailed deer weighs about 30% more than an adult female (Sauer, 1984). Because whole-body metabolic rate increases as the 0.7 power of body weight (Kleiber, 1975), while gut capacity increases linearly with body weight (Demment, 1982), males have a lower whole-body metabolic requirement per unit gut capacity than do females. This allows males to subsist on lower quality food, and, when abundance of high quality foods is limited, males have the option of expanding their diets to include lower quality but more abundant items. On the other hand, their relatively small gut capacity may not allow females to meet energetic needs by filling up on coarse, abundant foods.

McCullough's (1979) finding that the rumen contents of bucks had a higher dry weight relative to body weight is consistent with the above hypothesis. Also, Bowyer (1984) reported that southern mule deer females consumed *Sisymbrium*, a preferred food, in its earlier, more nutritious phenological stages. He suggested that the relatively larger rumen capacity of males might allow them, although feeding on phenotypically less desirable plants, to obtain a diet equal in nutrients to that of females.

The second explanation, spatial segregation of the sexes, seems to apply to most cases of resource partitioning in ungulates (Bowyer, 1984; Darling, 1937; Jackes, 1973; Murie, 1951; Shank, 1982; Takatsuki, 1980; Watson and Staines, 1978; Wehausen, 1980; Welles and Welles, 1961). In most of these studies, males occurred on poorer areas, although Wehausen (1980) and Shank (1982) found bighorn sheep (*Ovis canadensis*) rams on better ranges than ewes. Bowyer (1984) noted that although mule deer males tended to occupy areas with a lower abundance of preferred food, this was compensated by lower deer density on these areas so that availability of forage per individual deer did not differ significantly by sex. For white-tailed deer, McCullough (1979) reported that the sexes tended to segregate spatially on the George Reserve during the nonbreeding season, but segregation was fairly subtle. Nonetheless, if the areas used by each sex differ in food quality, even small differences could be important.

The small, consistent differences in diet quality reported herein are compatible with both of these hypotheses. However, the hypothesis that diet differences are due to the male's ability to subsist on poorer forage probably cannot explain the disjunction between recruitment rate and numbers of adult males reported by McCullough (1979). Because males would eat good foods when encountered, males would compete for the high quality foods that were sought by females. Accounting for the lack of correlation between recruitment rate and male numbers requires either that males pass up higher quality foods, or that the sexes forage in areas with different feeding opportunities.

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