Genetic and phenotypic parameters for dietary selection of mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb] Beetle) in Rambouillet sheep[1]

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ABSTRACT: The heritability of diet selection for mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb] Beetle) by grazing sheep was estimated from fecal samples collected from 549 Rambouillet ewes. Fecal samples were collected in September and October during 1996 and 1997 from free-grazing ewes on intermountain sagebrush-bunchgrass rangelands at the U.S. Sheep Experiment Station in Idaho. The total number of fecal samples was 1,949. Fecal samples were evaluated for composition of big sagebrush by near-infrared spectroscopy. Percentage of sagebrush in the diet was less in September than in October (21.6 vs 31.7%, respectively). Single-trait and bivariate derivative-free REML analyses were performed to genetically compare percentage of sagebrush in the diet in September and October. Heritability estimates were similar between September and October measurements (0.25 and 0.28, respectively). The genetic correlation between September and October percentages of sagebrush in the diet was high (0.91), implying that there is strong genetic similarity between September and October measurements and that an annual measurement may be sufficient for selection. These results contribute to a greater understanding of dietary preferences in freely grazing sheep, and suggest opportunities to improve production efficiency and forage management through selection for dietary preferences.

Key Words: *Artemisia*, Food Preferences, Grazing, Heritability, Sheep

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Introduction

Selection has long been used to develop different livestock breeds for production characteristics (milk, meat, and fiber), behavior, color, size, and resistance to disease, pests, or environmental extremes (Lasley, 1987). However, herbivores have not been purposefully bred for their diet characteristics. Selection and breeding of animals with specific diet characteristics could be used to develop livestock for vegetation management such as weed control or improved forage utilization.

Control of this important trait depends on an understanding of genetic and environmental factors influencing diet selection. Environmental factors shown to affect diet selection include learning (Provenza, 1996), grazing season, grazing pressure (Milne et al., 1979), and botanical composition of available forage (Launchbaugh et al., 1990). Although it is well established that species of livestock differ in diet selection (Grant et al., 1985), much less is known about the effect of variation within species. Two studies with limited numbers of observations have shown a significant sire effect for the botanical composition of diets of free-grazing goats (Warren et al., 1983) and cattle (Winder et al., 1995). Individual variation (i.e., the basis for genetic selection) in diet selection exists (Dove, 1935; Arnold and Dudzinski, 1978; Marinier and Alexander, 1991). Modifying diet preferences by genetic selection deserves attention because of the advantages of permanently incorporating the desired changes into an animal population. The objective of this study was to estimate heritability for percentage of mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb] Beetle) in the diet of Rambouillet sheep under range conditions.

Materials and Methods

This research was conducted at the U.S. Sheep Experiment Station located 10 km north of Dubois, ID

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Table 1. Average age (± SD), body weight, and number of observations on Rambouillet ewes sampled in September and October of 1996 and 1997

			Number of observations		
Year	Age, yr	Body weight, kg	September	October	Total
1996	2.6 ± 1.5	71.8 ± 8.0	543	540	1,083
1997	3.4 ± 1.3	74.5 ± 7.3	435	431	866

(112°10′W, 44°21′N), which is a research unit of the USDA Agricultural Research Service. During the study, sheep grazed on sagebrush-grasslands that have been typically used as spring and fall range.

Animals and Management

This study measured percentage of sagebrush in the diet of Rambouillet sheep, a typical western white-faced, fine-wool sheep breed. Data on the percentage of sagebrush in the diet were collected on a total of 549 ewes over 2 yr, resulting in an unbalanced repeated measures design. The ewes originated from 100 sires. Live body weight of the animals averaged 72 to 75 kg (Table 1). Data were collected on the same animals in both years, resulting in a higher average age of the ewes in the 2nd yr (Table 1). The slightly lower number of animals in the 2nd yr of the study reflects normal culling and death loss.

Ewes had been separated from their lambs approximately 3 wk before the first fecal collection period. Weaning occurred while the ewes and lambs were summer grazing on high-elevation (2,590 m) conifer-forested meadows. Ewes were then trailed to lower-elevation (1,700 m) sagebrush grasslands, which they grazed continually for approximately 3 wk prior to the first sampling period in September. Water and a granulated salt mineral mix were provided to the ewes for ad libitum consumption. This management process was repeated in the 2nd yr of the study.

Because previous research on a Targhee line selected for litter weight weaned at the U.S. Sheep Experiment Station suggested that greater dry matter intake was associated with lactation under range conditions (P = 0.14; Head et al., 1995), genetic lines within the Rambouillet breed were considered for statistical analyses. Three genetic selection lines exist within the Rambouillet breed at the U.S. Sheep Experiment Station: 1) a wool line selected for heavier fleeces with a threshold for maximum fiber diameter, 2) a maternal line selected for total litter weight weaned, and 3) a random-bred control line. Ewes were bred to single sires within selection lines. Parental identification was ascertained by continual observation during the lambing season. Pedigree ties across lines had been created previously by infrequent breeding of rams from the control line in the selected lines that had excelled in the selected trait(s), but this practice ended 8 yr before this study.

Sagebrush Grassland

Vegetative composition of the study range was estimated from soils survey data (NRCS, 1995) based on dry matter production at peak biomass. Sagebrush communities were on predominantly loam-type soils and were dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp *vaseyana*; 15 to 45% composition by weight). Other abundant woody species included threetip sagebrush (*Artemisia tripartita*) and bitterbrush (*Purshia tridentata*). The dominant herbaceous plant was bluebunch wheatgrass (*Pseudoregneria spicata*; 20 to 40% composition by weight); other grasses included Idaho fescue (*Festuca idahoensis*), sandberg bluegrass (*Poa sandbergii*), and thickspike wheatgrass (*Agropyron dasystachyum*). Grasses contributed 50 to 60% of the annual forage biomass and, though dormant by the time of the study, they still constituted most of the available biomass. Forbs contributed 10 to 20% of the annual forage biomass of the area and consist mainly of arrowleaf balsamroot (*Balsamorhyiza sagittata*), tapertip hawksbeard (*Crepis acuminata*), velvet lupine (*Lupinus leucophyllus*), and dozens of other species in trace amounts. By fall, when the trial was conducted, the forbs had senesced and decomposed, so they were largely unavailable.

These rangelands were grazed by ewes and their lambs under herded conditions in the spring (May and June) and again by the ewes after fall weaning (September and October). Although ewes were under the constant surveillance of a herder, they had free access to the vegetation. Grazing constraints related to diet selection imposed by the herders were considered minimal because sheep were moved frequently (generally every 2 to 4 d) to new grazing sites within the rangeland (3,148 ha), which prevented overgrazing and allowed the sheep free choice among existing vegetative species. Therefore, diet selection for sagebrush was considered to be based on an individual animal's choice rather than being influenced by grazing pressure or forage availability.

Stocking rates maintained in 1996 and 1997 were well below a moderate rate to ensure that availability of sagebrush or herbaceous biomass did not restrict intake during the study. The low to moderate stocking rate for the study pasture, based on estimates by the Natural Resource Conservation Service (NRCS, 1995), is 0.78 AUM/ha for an average rainfall year. The actual stocking rate in 1996 was 0.06 AUM/ha for the spring grazing period and 0.1 AUM/ha for the fall period; and in 1997, the stocking rate was 0.09 AUM/ha for spring grazing and 0.09 AUM/ha for the fall grazing period. Average annual precipitation for the study area is 30 to 35 cm, and in the years of the study precipitation was 33 cm in 1996 and 32 cm in 1997.

Fecal Sample Collection and Analyses

The percentage of sagebrush in the diet was determined by analysis of fecal samples with near-infrared reflectance spectroscopy (**NIRS**) according to the procedure of Walker et al. (1998). Fecal samples were collected from the rectum of each ewe on two consecutive days in September and again in October. Fecal samples were collected midmorning on September 24 and 25 and October 8 and 9 in 1996 and 1997. Within 6 h of collection, samples were dried in a forced-air oven at 55°C for 48 h. Duplicate dried fecal samples were composited by individual animal within sampling month and year and stored at room temperature in paper bags. Composite samples were ground in a cyclone mill (UDY Corp., Fort Collins, CO) to pass a 1-mm screen. Ground samples were stored in small Whirlpak plastic bags at room temperature until they were evaluated.

Near-infrared spectroscopy evaluations were performed on each composite sample using a NIR Systems (Silver Spring, MD) model 6500 scanning reflectance quartz cover glass. Reflected energy (log 1/R) was measured, averaged over 32 scans, and recorded at 2-nm intervals from 4,400 to 2,500 nm. A personal computer, interfaced to the monochromator, used ISI NIRS2 version 3 software (Infrasoft International, Port Matilda, PA) to collect spectra and predict the percentage of sagebrush in the diets. The equation contained five near-infrared wavelengths and had an R^2 of 0.95 and standard error of validation of 2.3%. The NIRS calibration equations to predict sagebrush in sheep diets from fecal samples were developed from feeding trials separate from this study. The calibration equations were validated by applying them to samples different from those used for calibration. For validation, the prediction equation accounted for 90 to 95% of the variation, and animal within diet accounted for 4% of the variation (J. W. Walker, unpublished data). Furthermore, Walker et al. (1998) found that NIRS was more accurate than the microhistological method for estimating the amount of leafy spurge (*Euphorbia esula* L.) in sheep diets.

Statistical Analyses

The statistical difference between September and October percentages of sagebrush in the diet was tested using the Tukey-Kramer method with the GLM procedure of SAS (SAS Inst. Inc., Cary, NC). The model was an unbalanced repeated measures design. Samples from ewes were collected across months and years, but not all ewes were present in both years and some samples could not be collected. The fixed effects included months (September vs October), year of collection (1996 and 1997), genetic selection line (wool, maternal, and random control), and age of the ewe (2, 3, and > 3 yr of age). Body weight of the ewe at weaning was included as a linear covariate.

Genetic analyses of the data required identification of the genetic relationships among all ewes in the study. This was accomplished by using the MTDFREML subroutine procedure found in the computer programs of Boldman et al. (1993). The genetic relationship matrix was generated from the Rambouillet pedigree file from 1975 to 1997, totaling 3,261 animals from 404 sires and 1,953 dams. The average inbreeding coefficient was small (1.9%); therefore, the effects of inbreeding on the percentage of sagebrush in the diet were assumed to be negligible.

Variance components for September and October percentages of sagebrush in the diet were estimated using single- and two-trait statistical analyses. The two-trait analysis estimated genetic and environmental correlations between measurements in September and October. Estimates of variance and covariance components were obtained using a derivative-free REML algorithm (Graser et al., 1987) with the computer programs of Boldman et al. (1993). Convergence was considered to have been reached when the variance of the −2 log likelihood in the simplex was less than 1×10^{-6}. After initial convergence, six restarts were performed to ensure global convergence determined by when the −2 log likelihood did not change to the second decimal.

Single-trait analyses were performed for each month of measurement (September or October). The model included as fixed effects year of measurement (1996 and 1997), genetic selection line (wool, maternal, and random control), and age of ewe (2, 3, and > 3 yr of age). Body weight of the ewe at weaning was included as a linear covariate. Random effects included additive genetic effect of the ewe and permanent environmental effect of the ewe to account for repeated measurements. Because estimates of the additive genetic variance component for the percentage of sagebrush in the diet were previously unknown, prior values for the analyses were initially based on a heritability estimate of 0.3 reported for diet selection in goats (Warren et al., 1983).

A two-trait analysis was performed to determine the genetic correlation between measurements in September and October of percentages of sagebrush in the diet. The model included the same effects as those in the single-trait model plus all possible covariances between additive genetic and permanent environmental effects for the two periods of measurement.

Results and Discussion

Estimates of the average percentage of sagebrush in the diet as measured by NIRS on fecal matter did not differ across years of collection ($P = 0.56$; Table 2) but did differ between months of collection ($P = 0.001$). Sagebrush represented 21.6% of the diet during September and increased to 31.7% in October. All ewes consumed some sagebrush. The range between minimum and maximum percentage of sagebrush in the diet was two- to threefold.

Sagebrush has frequently been reported to be an important forage plant for sheep. Cook et al. (1948) reported that Rambouillet sheep consumed 38.6% sagebrush-type browse in the northern central Utah mountains, where sagebrush cover was estimated be 34% during summer grazing (mid-July to mid-September). Big sagebrush (*Artemisia tridentata*) consumption has exceeded 90% of the diet in Rambouillet-type sheep grazing sagebrush on winter (November to April) range in central Utah, where sagebrush composed about 93% of the biomass (Cook and Harris, 1950). On sagebrush-grass rangelands where browse constituted 50% of the herbage production, big sagebrush composed only 5% of sheep diets from September to April (Cook and Harris, 1968). The higher percentage of sagebrush in October than in September diets was consistent with the generally observed increase in browse utilization by sheep as the grazing season progresses on intermountain rangelands (Cook and Harris, 1968). The increased percentage of sagebrush in the diet presumably represents the increased value of this forage compared to other alternatives as the grazing season progresses (Newman et al., 1995).

The nutritive value of big sagebrush as a forage for sheep generally exceeds the requirements for nonlactating mature ewes (Welch, 1981). On a dry matter basis, the chemical composition of big sagebrush is approximately 60% TDN, 12% crude protein, 0.65% calcium and 0.20% phosphorus (Cook and Harris, 1950; Welch, 1981). Welch and McArthur (1979) found percentages of crude protein ranging from 8 to 17% in differing accessions of big sagebrush and suggested that nutritionally superior lines of big sagebrush could be developed for use on sheep and mule deer ranges.

The percentage of sagebrush in the diet was not different among Rambouillet selection lines. Estimates of variance components from single-trait analyses were similar to those from bivariate analysis; therefore, only estimates from the bivariate analysis are presented in Table 3. Heritability estimates were similar for measurements in September and October (0.25 and 0.28, respectively). In a 2-yr study that investigated heritability of diet selection of Spanish goats based on half-sib analysis of 155 goats from 14 sire groups in western Texas, Warren et al. (1983) concluded that there was no effect of sire for diet preference for the most commonly consumed forage species. However, average heritability for percentage dietary composition of the least commonly consumed forage species was 0.30. In the Warren et al. (1983) study, sagebrush would also be considered among the less commonly preferred forages. Winder et al. (1995), who investigated the genetic aspects of diet selection of Brangus cows in the Chihuahuan desert in New Mexico, found significant sire effects for botanical composition of several plant species or genera in fall diets but not in winter or summer diets. Their heritability estimates, derived from a small number of sires ($n = 12$), ranged from 0.51 to 0.87 with standard errors of approximately 0.5. Heritability estimates in our study were based on 1,949 diets from 549 ewes out of 100 sires. As a comparison, heritability for weaning and yearling weight in ancestors to the sheep in this study were 0.45 and 0.57, respectively (Ercanbrack and Price, 1972).

Environmental effects represented approximately 70% of the phenotypic variation for each month of measurement. The large contribution of environmental effects to the variance of diet composition was expected because of the many biological factors influencing big sagebrush availability and palatability. The correlation between September and October environmental, or residual, effects was small ($r = 0.16$), implying little overlap of environmental effects on the ewes for the 2 mo. Permanent environmental effects associated with repeated measurements on ewes made up less than 4% of the phenotypic variance.

The genetic correlation between percentages of sagebrush in the diet for September and October measurements was 0.91. A genetic correlation greater than 0.85 strongly implies that the two traits are genetically similar (Robertson, 1959). Therefore, preference for percentage of sagebrush in the diet seems to be genetically similar between September and October measurements, even though the average percentage of sagebrush in the diet was one-third greater in October than in September. Response to selection for the per-

Table 2. Means (± SD) and minimum and maximum percentages of sagebrush (*Artemisia tridentata*) in the diet of Rambouillet ewes

	September			October		
Year	Mean	Min.	Max.	Mean	Min.	Max.
1996	23.4 ± 2.4[a]	17.4	31.9	32.7 ± 2.9[b]	23.7	42.3
1997	19.5 ± 2.6[a]	10.3	28.4	30.4 ± 2.5[b]	23.6	39.6
Total	21.6 ± 3.2[a]	10.3	31.9	31.7 ± 3.0[b]	23.7	42.3

[a,b]Within a row, means without a common superscript letter differ ($P < 0.05$).

Table 3. Estimates of variance components and fractions[a] of total variance for percentage of sagebrush in the diet of Rambouillet sheep from bivariate analysis

Month	σ^2_a	σ^2_{pe}	σ^2_e	σ^2_p	h^2	pe^2	e^2
September	1.57	0.00	4.79	6.36	0.25	0.00	0.75
October	2.02	0.27	5.04	7.34	0.28	0.03	0.69

[a] σ^2_a, additive genetic variance; σ^2_{pe}, permanent environmental variance; σ^2_e, residual variance; σ^2_p, total variance; h^2, fraction of total variance represented by σ^2_a; pe^2, fraction of total variance represented by σ^2_{pe}; e^2, fraction of total variance represented by σ^2_e. Genetic correlation between measurements in September and October, 0.91. Permanent environmental correlation, 0.00. Residual correlation, 0.16.

centage of sagebrush in the diet should be similar whether genetic selection is based on measurements made in September or October. Also, the correlation between the random permanent environmental effects of the ewe was inconsequential (r = 0.003), indicating that the nongenetic effects associated with the ewe across sampling months were not important.

Genetic influences on diet selection have been investigated in mice (McClearn and Rodgers, 1961; Lush, 1981), humans (Krondl et al., 1983), goats (Warren et al., 1983), and cattle (Winder et al., 1995). However, genetic mechanisms affecting diet selection are only beginning to be understood. Recent studies have indicated that genes play an important part in physiological mechanisms affecting food preferences, such as taste sensitivity, enzyme deficiencies associated with nutrient intolerance, and detoxification of chemicals. Studies in mice have demonstrated that genetic influences on dietary intake can be additive, recessive, dominant, or pleiotrophic (Bachmanov et al., 1996, 1997). Gene mapping research has identified loci in mice associated with the neural response to sensory taste factors for several chemicals, including sweetness of the amino acid phenylalanine (Nimomiya et al., 1991), saccharin, sucrose, and quinine (Blizard et al., 1999). In humans, genetic factors influence dietary preference via taste sensitivity. Acceptance or rejection of broccoli by humans has been linked to strong genetic influences on taste sensitivity to the bitter flavor associated with phenylthiocarbamide (Krondl et al., 1983). Genetic factors have also been found to influence preference for hamburger, cottage cheese, chicken, and orange juice by humans (Falciglia and Norton, 1994). In humans, the inability to digest certain foods has been linked to genetic influences on enzyme deficiencies; the most well-known human enzyme deficiency is lactase (Lisker, 1984) but may also include fructose intolerance and galactosemia. Research to identify similar genetic factors influencing the grazing ruminant's preference is needed with potential application to animal nutrition, forage utilization, and biological control of noxious weeds.

In a practical sense, the heritability estimate for percentage of sagebrush in the diet (0.25 to 0.28) is moderate, implying that the trait will respond to selection pressure. The rate of response will depend on selection pressure placed on the trait. A one-percentage-point increase of sagebrush in the diet per generation could be achieved if 20 animals out of a population of 100 were selected for breeding based on percentage of sagebrush in their October diet (where selection intensity factor = 1.4, phenotypic standard deviation = 2.7, and heritability estimate = 0.28 for October measurements).

The concept that diet selection may be an important trait is relatively new (Walker, 1995; Launchbaugh et al., 1999). Selective breeding for characteristics of diet selection could be used to improve the value of livestock for vegetation management. Use of livestock to control undesirable plants is dependent on their grazing of the target plant at a level that will place that species at a competitive disadvantage relative to other plants in the community. For example, sheep grazing is routinely used to help manage leafy spurge (*Euphorbia esula* L.; Johnston and Peake, 1960) and three-tip sagebrush (*Artemisia tripartita* Rydb; Laycock, 1967).

Although selection may increase sagebrush utilization among sheep, physiological limitations to sagebrush intake may occur. Sudden high exposure to big sagebrush can result in severe necrotizing rumenitis and eventual death (Johnson et al., 1976). Consumption of big sagebrush may also predispose sheep to photosensitization (bighead) caused by subsequent intake of horsebrush (*Tetradymia canescens*; Johnson, 1974). The presence of terpenes, toxic to ruminal microbes, in sagebrush can depress in vivo digestibility (Ngugi et al., 1995) and thus reduce intake (Burritt et al., 2000). Several studies have reported that sheep adapted to big sagebrush winter ranges and consuming at least 20% sagebrush on a dry matter basis did not exhibit negative physiological effects (Cook et al., 1948; Cook and Harris, 1950; Welch, 1981). Further studies are needed to understand the physiological effects of increasing sagebrush intake on animal health and productivity.

As the economic and social importance of noxious weeds increases, use of livestock to help control these weeds can become an important selection criterion for breeders. In the United States, the annual cost of controlling noxious weeds and lost production due to weed infestation is estimated to be $12 billion (Babbitt, 1998), compared to a total estimated value of sheep and lambs of $640 million (USDA-NASS, 1999). Thus, the direct cost of noxious weeds is 18 times greater than the total value of the sheep industry. Although sheep could never be the sole solution to the noxious weed problem, if sheep reduced the problem by only 5%, the value of sheep would be double their current total economic value.

Implications

This study confirms that genetic factors significantly influence dietary preferences of grazing sheep for a single plant species, mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb) Beetle). Selective breeding to manipulate dietary preferences of ruminants may lead to improved animal production by producing animals with inherent preferences for more nutritional plants. Genetic manipulation of dietary preferences for target plant species may also result in more desirable forage utilization and biological control of noxious plants. Whereas ruminants have long been used as harvesters of forage, in the future, utilization of ruminants as managers of forage through their selective dietary preferences may become increasingly important. The ultimate value of sheep production in the United States may depend on the sheep's ability to reduce the annual $12 billion loss due to noxious weeds.

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