Heritability of juniper consumption in goats[1]

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ABSTRACT: Data from goats (n = 505), collected over a 4-yr period, were used to estimate the heritability of juniper consumption. Juniper consumption was determined by near-infrared spectroscopy on fecal samples (n = 1,080) collected from female Boer-cross goats grazing pastures with a variety of plants, including juniper. The animals with records were progeny of 72 sires. Individual goats had from 1 to 4 observations over a 4-yr period. Predicted juniper consumption for individual observations ranged from −5 to +62% of the diet. Data were analyzed with a mixed model that included management group as a fixed effect, BW as a covariate, and permanent environment, animal, and residual as random effects. Management group was a significant source of variation. Least squares means of juniper consumption, as a percentage of the total intake, for management groups varied from 19 to 47%. Heritability of juniper consumption was 13%. Repeatability of juniper consumption was 31%. These results suggest that progress to selection for goats that will consume greater amounts of juniper is obtainable, but is expected to be slow.

Key words: diet selection, goat, juniper

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INTRODUCTION

The use of small ruminants to provide environmental services such as weed control and landscape management is becoming increasingly important (Popay and Field, 1996; Martyniuk and Olech, 1997). Dense stands of Ashe's (*Juniperus ashei* J. Buchholz) and Pinchot's (*Juniperus pinchotii* Sudw.) juniper reduce forage production and plant diversity, interfere with handling and movement of livestock, degrade wildlife habitat, increase volatile fuel loads, and reduce the availability of water (Hamilton and Ueckert, 2004). Because of the negative consequences of juniper encroachment, juniper is considered to be the largest economic and ecological problem facing land management in the Edwards Plateau today (Taylor, 2008). By preferring some plant species and avoiding others, free-grazing livestock significantly affect the botanical composition and biodiversity of natural plant communities. Browsing by goats can effectively reduce encroachment of juniper on rangelands that have been cleared by mechanical or pyrrhic control methods (Taylor, 2008). Monoterpenes in juniper limit consumption by animals (Riddle et al., 1996). In a review of the use of livestock to manage vegetation on pastures, Rook et al. (2004) identified the need to determine the extent that elements of foraging behavior and selectivity are genetically determined. Ellis et al. (2005) reported genetic variation, within a population, for juniper consumption measured when goats were in a pen. Snowder et al. (2001) documented genetic variation for diet selection in grazing sheep. If sufficient genetic variation exists in goat populations, it may be feasible to select for goats that consume greater amounts of juniper. The selected population would have increased effectiveness for sustainable, low-cost juniper control. An estimate of heritability is one of the parameters needed to predict expected response to selection. The objective of this study was to estimate heritability for juniper consumption within a herd of goats by using near-infrared spectroscopy (**NIRS**) determinations of juniper consumption.

MATERIALS AND METHODS

All procedures involving animals were approved by the Texas A & M University Institutional Agricultural Animal Care and Use Committee.

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Animals

A herd of mixed-age Boer-cross goats was maintained by the Texas Agricultural Experiment Station at a ranch in Edwards County, Texas. Vegetation on the ranch is characterized by dense, scattered live oak (*Quercus virginiana* Mill.) mottes with grass interspaces. The midgrass component of the grass interspaces is dominated by sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] and Wright's threeawn (*Aristida wrightii* Nash). Other important midgrasses include fall witchgrass [*Leptoloma cognatum* (Schult.) Chase], Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.), and silver bluestem [*Bothriochloa saccharoides* (Sw.) Rydb.]. Short grasses that are predominantly common are curly-mesquite [*Hilaria belangeri* (Steud.) Nash] and red grama (*Bouteloua trifida* Thurb.). Honey mesquite (*Prosopis glandulosa* Torr.), Ashe's juniper, and Pinchot's juniper are prominent woody species that are scattered through the grass interspaces in a savanna-like fashion. Prickly pear (*Opuntia* spp. Mill.) is also abundant. Numerous species of annual forbs are also present when adequate soil moisture is available during the fall and early winter.

Animals were maintained on pasture throughout the year, except for late gestation and early lactation. Mature females were exposed to bucks for breeding in May and June and again in September and October each year. Therefore, a portion of the herd kidded in October and November and another portion kidded in February and March.

Individual animal fecal samples (n = 1,080) were collected over a 4-yr period (2002 to 2005). All fecal samples were obtained in the winter between January 28 and February 28, and all animals were female. The winter was chosen because Malechek and Leinweber (1972) showed that goats ate more juniper in the winter than in other seasons. Therefore, at the time the fecal samples were obtained, mature females consisted of those that had kidded to the May to June mating and those that were pregnant from the September mating. Yearling does, which had not been mated, were also sampled. All animals were gathered from pastures on the morning of the day of fecal collection. All samples from goats within a management group were collected on the same day. The fecal samples came from 505 different goats, which were progeny of 72 different sires. The goats ranged from 1 to 9 yr of age at the time of collection (Table 1). Individual goats had from 1 to 4 observations over the 4-yr period (Table 2). The mean BW across all years was 50 kg. The BW of the yearlings and mature does ranged from 22 to 51 kg and 27 to 85 kg, respectively. Mean BW by management group is shown in Table 3. Management groups (n = 10) were age group (yearling or mature) × pasture combinations. Each management group contained from 71 to 203 animals (Table 3). Although management groups were in different pastures, all pastures were similar with respect to juniper availability, which greatly exceeded animal demand. Pastures were also similar with respect to other available forage.

Table 1. Number of fecal samples for near-infrared spectroscopy determination of percentage of juniper in goat diets collected over a 4-yr period by age of goat

Age, yr	Samples
1	315
2	212
3	154
4	87
5	44
6	40
7	57
8	98
9	73

Laboratory Analysis

Fecal samples were dried in a forced-air oven (50°C for 48 h), ground in a cyclone mill to pass through a 1-mm screen, redried in a forced-air oven (50°C for 12 h), and conditioned for 24 h in an environment with constant temperature and relative humidity (21°C, 65%). Approximately 4 g of ground, conditioned samples were packed into sample cells with a near-infrared transparent quartz cover glass (Foss NIRSystems, 2000). Cells were scanned 32 times using a model 6500 scanning reflectance monochromator (Foss NIRSystems Inc., Silver Spring, MD). Reflected energy (log 1/R, where R = reflectance) was measured and averaged over the 32 scans and recorded at 2-nm intervals from 1,100 to 2,500 nm. The calibration equation (r^2 = 0.88 and SE of cross validation = 6%) used to determine percentage of juniper in the goat diets from the fecal spectra was the same as the independent equation used by Walker et al. (2007). This equation was shown to provide precise, but potentially biased, estimates of juniper in the diet, and the predictions should be considered an interval scale of measurement.

Statistical Analyses

A mixed model analysis was conducted using the NIRS determinations of percentage of juniper in the diet as the phenotypic observation. The mixed model included collection date-management group as a fixed

Table 2. Number of fecal samples per goat for near-infrared spectroscopy determination of percentage of juniper in goat diets

Samples	Goats
1	159
2	178
3	107
4	61

Table 3. Descriptive statistics for fecal near-infrared spectroscopy (NIRS) determination of percentage of juniper in goat diets by management group

						Fecal NIRS		
Group	Year	Age	n	Avg BW, kg	SD	Mean, %	Minimum, %	Maximum %
A	2002	Mature	72	55	7	37.7	24	54
B	2002	Yearling	75	38	5	43.1	32	53
C	2003	Mature	156	53	7	27.0	−2	61
D	2004	Mature	181	57	9	19.4	2	37
E	2004	Yearling	80	39	7	22.7	12	35
F	2005	Mature	203	51	10	22.4	−5	47
G	2005	Yearling	88	40	5	37.3	20	56
H	2002	Mature	82	53	9	30.6	15	45
I	2003	Mature	71	59	7	37.8	16	57
J	2003	Yearling	72	40	6	51.0	37	62

effect, BW as a linear covariate, and random effects for animal genetic effect, animal permanent environmental effect, and residual. The relationship matrix included the 505 animals with observations and additional relatives without observations. Variance components were estimated using ASREML software (Gilmour et al., 2002). Heritability was calculated as the additive genetic variance estimate divided by the phenotypic variance estimate. Repeatability was calculated as the sum of the additive genetic variance and the permanent environmental variance divided by the phenotypic variance.

RESULTS AND DISCUSSION

The mean predicted percentage of juniper in the diet was 30, with a SD of 12, and ranged from −5 to +62%. Fecal NIRS predictions should be interpreted as an interval scale of measurement, where differences among observations have meaning but there is not a true zero point (Walker et al., 2007). Management group was a significant source of variation. Estimates of management group means for juniper consumption ranged from 19 to 47% of the diet. Variation in management group means of dietary consumption of juniper can be due to year differences in forage quantity, quality, and relative availability of different forage species because of annual variation in precipitation and temperature. The amount and quality of forage are a function of previous precipitation, temperature, and stocking rate (current as well as past). The estimated regression of juniper consumption on BW was not significantly different from zero ($P > 0.1$). Because juniper consumption was expressed as a percentage of the diet, this result was not unexpected.

Differences in juniper consumption attributable to production status and management group need to be accounted for to make valid comparisons among animals. Factors that affect juniper consumption are not well understood.

Variance component estimates are shown in Table 4. The heritability estimate was 13% and the repeatability estimate was 31%. Of the several studies that have estimated heritability of the botanical composition of diets of domestic livestock, the study by Snowder et al. (2001) is most similar to the current study. Both the current study and that by Snowder et al. (2001) are similar in that they contained relatively large numbers of observations and sire groups; the variable of interest was percentage of a relatively unpalatable woody plant (juniper and sagebrush, respectively) that contains monoterpenes as feeding deterrents, and fecal NIRS was used to determine percentage of the target plant in the diets of the animals. Snowder et al. (2001), using data from 549 ewes from 100 sire groups, reported heritability estimates of 25 and 28% for percentage of sagebrush in the diet of Rambouillet ewes in September and October, respectively. Estimated heritability for percentage of sagebrush in sheep diets was approximately double our estimate for heritability of percentage of juniper in goat diets, whereas the phenotypic SD was more than 2 times as great in this study as in the study by Snowder et al. (2001), and the residual environmental effects represented approximately 70% of the phenotypic variation in both studies.

The heritability estimate of juniper consumption for 3 annual cohorts of Boer-cross kids offered juniper branches in a pen-feeding scenario ranged from 0 to 46% and was 11% when calculated across all 3 yr (Ellis et al., 2005). Warren et al. (1983), using microhistological estimates of diet botanical composition, reported that sire (14 sire groups) was a significant source of variation for 18 of 33 plant species. Juniper was 1 of the

Table 4. Variance component and genetic parameter estimates for percentage of juniper in the goat diets

Item	Estimate	SE
Additive, $\%^2$	6.58	3.02
Permanent environmental, $\%^2$	9.19	2.17
Residual, $\%^2$	35.81	17.41
Phenotypic, $\%^2$	51.56	
Heritability, %	12.8	5.7
Repeatability, %	30.6	3.8

18, but juniper consumption was less than 1% of the diet and juniper was much less abundant than in the pastures used in the present study. Nevertheless, their data showed evidence of significant genetic variation for diet selection for several plants.

Although the data sets used to assess the genetic variation for diet selection vary in size, none of them, including the present study, can be considered large for the purpose of parameter estimation. Therefore, further studies of diet selection are warranted to obtain more reliable estimates of genetic parameters.

In several goat-grazing studies that spanned different years or seasons, it has been shown that substantial changes in diet are a result of available choices (Askins and Turner, 1972; Malechek and Leinweber, 1972; Warren et al., 1983, 1984). In the present study, we assumed that we were “measuring” the same trait (percentage of juniper in the diet) each winter. Snowder et al. (2001) estimated the genetic correlation between September and October measurements of percentage of sagebrush in sheep diets as 0.91, even though sagebrush was 21.6% of the diet in September and 31.7% of the diet in October. Because the number of animals with observations for each of the 4 yr of this study was small, we did not estimate the genetic correlation among multiple measurements. However, if the environmental variation across years was large enough to invalidate this assumption, and if this resulted in a genotype $\times$ environment interaction, our heritability estimates would be biased downward.

In this study, in addition to the normal annual variation in diet selection, 3 potential sources of variation could contribute to the residual variation, namely, 1) the effect of different years and cohorts on fecal spectra (Walker et al., 2007); 2) cyclic periodicities in juniper consumption (Campbell et al., 2007); and 3) nongenetic maternal influences on diet selection.

In addition, fecal spectra can vary and cause biases in the determination of percentage of juniper in the diet because of the sex of the animals, age of the animals, and diet (Walker et al., 2007). However, because all animals in the current study were females and $\geq$1 yr old, these potential sources of variation can be considered negligible. Variation in the botanical composition of the diets for the nonjuniper species probably did cause biases among the different management groups, but deviations from the management group mean for individuals within a group are probably not greatly affected by the effect of management group on the fecal spectra. Because the precision of fecal NIRS determinations of dietary botanical composition is relatively great (Walker et al., 2002, 2007), we do not believe that the methods for estimating percentage of juniper in this study biased the results.

Goats on the same pasture vary in their consumption of juniper both seasonally and intraseasonally (Campbell et al., 2007). Cyclic intraseasonal variation in chemically defended plants is presumably a cybernetic response to mediate consumption of aversive plant secondary compounds (Pfister et al., 1997) such as monoterpenes. Intraseasonal variation of juniper consumption could contribute to either the permanent environmental or the residual effect and reduce the estimated heritability of percentage of juniper in the diet. This would occur if all animals were not measured at the same point in their intraseasonal cycle. This most likely occurred in this study because all animals within a management group were measured once on the same day and because these intraseasonal cycles are probably not synchronized among animals. Sampling several times each season, to more accurately estimate percentage of juniper in the diets, might have changed the estimated variance components in this study.

Diet selection of an individual can be affected by the dietary habits of the dam, and this is generally considered a learned behavior (Thorhallsdottir et al., 1990a,b; Mirza and Provenza, 1992) as opposed to being genetically determined. This early work on learning and social models was done in controlled pen studies, and results from field trials have been less conclusive (Salem et al., 2005; Whitney and Olson, 2006). Nonetheless, the potential exists for learned behaviors to interact with an inherited ability to avoid negative feedback from chemically defended plants, which would not only affect the heritability, but also would need to be considered in breeding programs for modifying diet selection. A better understanding of genetic and environmental effects, such as learned behaviors, will be important for making genetic progress for modifying diet selection. The 505 animals with observations in this data set were the progeny of 322 dams. The majority of the dams were represented by only one offspring. Only 14% of the dams had more than 2 progeny with records. Therefore, because of the limited information, we chose not to include maternal genetic and maternal permanent environmental terms in the model. A larger data set or a data set with more progeny per dam, or both would be more appropriate for estimating maternal effects.

The heritability values from the present study indicate that progress from selection has the potential to change the population, but not rapidly. The theoretical expected response to selection is given by the product of the heritability and the selection differential. It is feasible to select males that are 2 phenotypic SD above the mean. If no selection is practiced on the female side, the selection differential is equal to 1 phenotypic SD (approximately 7% = square root of 51.56). The expected response to selection is then approximately 1% per generation. A generation interval of 2 yr would result in progress attributable to selection of 0.5%/yr. This expected response is similar to that calculated from the results of Snowder et al. (2001), who reported greater heritability and smaller phenotypic variance. If no physiological factors are limiting selection progress, a 10-yr selection program could result in a 5% increase in mean juniper consumption.

An estimate of heritability is only one component needed to predict progress from selection. The present analysis is part of an ongoing research project that has the objective of identifying differences among animals in diet selection and their subsequent impact on undesirable plants. The authors have initiated a divergent selection project to estimate progress from selection and to generate differences among animals, to improve our power to identify physiological differences that might explain variation in juniper consumption. If selection progress leads to substantial differences in juniper consumption, or a physiological test can be identified that will allow screening of large populations for extreme animals with respect to juniper consumption, herds of selected goats could be produced that would be much more effective at controlling juniper.

If the anticipated increased demand for the ecological value of grazing livestock is realized, the ability to manipulate diet selection both genetically and environmentally will become increasingly important. Snowder et al. (2001) noted that the value of sheep for controlling invasive plants could exceed the value of the food and fiber they produce. Knowledge of the heritability and repeatability of juniper consumption is needed to design an efficient selection program. Genetic variation for juniper consumption is such that selection can be used to change the mean value of a population.

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