

# Effects of domestic goats on deer wintering in Utah oakbrush

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## Abstract

Dietary composition and quality, activity budgets, and foraging behavior of tame mule deer (*Odocoileus hemionus hemionus*) were monitored in winter to ascertain the effects of prior summer use of oakbrush communities by domestic goats (*Capra hircus*). Reduction of deciduous browse by goats resulted in increased use of Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle and Young) by deer when snow cover precluded use of understory species. As a result, the diets of deer confined to goat-browsed pastures contained less fiber and tannins, and were more digestible than those of deer in control pastures. Digestible protein in diets did not differ. No goat-related effects were observed in the absence of snow because deer grazed the herbaceous understory which had not been substantially altered. Quality of cured herbage was low, and deer did not effectively select for fall regrowth. Consequently, diet quality under snow-free conditions was not substantially different from that observed under snow-covered conditions. Snow reduced foraging efficiency; deer travelled faster, and exhibited lower bite and intake rates when feeding under snow-covered conditions than under snow-free conditions. Goat-induced vegetal differences were not reflected in activity budgets or foraging behavior, regardless of snow condition. We conclude that goats may be used to periodically manipulate composition of oakbrush winter range, thereby enhancing quality of deer diets under snow-covered winter conditions. However, enhancement of deer diets under snow-free winter conditions probably requires annual manipulation of the understory.

**Key Words:** *Odocoileus hemionus hemionus*, *Capra hircus*, forage-base change, winter food habits, nutritional plane, activity budgets, foraging efficiency

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Management of oakbrush for game winter range has historically focused on successional advanced stands in which Gambel oak (*Quercus gambelii* Nutt.) has attained dominance. Oak typically has grown beyond reach in these stands and suppressed subordinate species, thereby reducing availability of forage for wintering ungulates. Such stands are generally managed with fire, herbicides, or mechanical treatment. All shrubs are initially reduced, and Gambel oak apparently responds more aggressively than associated species (Kufeld 1983). Availability of oak browse is enhanced. However, more nutritious subordinates, such as big sagebrush (*Artemisia tridentata* Nutt.), are reduced. Consequently, average quality of the available forage can actually decline.

As an experimental alternative, Spanish-type domestic goats (*Capra hircus*) have been used to alter shrub composition before oak attains dominance. The treatment involves periodic high-intensity browsing during the growing season, and results in enhancement of sagebrush via disproportionate use of associated deciduous browse (Riggs et al. 1988, Riggs and Urness 1989). Wintering ungulates may benefit from the goat-induced composition shift if they adjust their diets and do not incur compensatory energetic costs associated with securing or processing forage. In this paper, we examine the responses of wintering mule deer to goat-induced vegetal change in terms of diet composition and quality, foraging efficiency and activity budgets.

## Methods

### Experimental Setting

The experiment was conducted on a remote oakbrush winter range community in northern Utah. Gambel oak was dominant but still within browsing reach of goats and deer. This community was subdivided into 6, 0.2-ha pastures arranged in 3 blocks; each block contained 1 control pasture and 1 treatment pasture that was stocked with goats. The stocked pastures received 1,340 goat-days use per ha in 1984, and 1,840 goat-days in 1985. Goat use was applied in repeated high-intensity, short-duration browsing periods that were aimed at maximizing defoliation of Gambel oak (Riggs and Urness 1989).

The responses of wintering deer to goat-induced community changes were evaluated during the subsequent 2 winters. Snow

conditions differed between years. Snow depth was about 230 mm in 1985; this amount of snow hampered use of the smaller shrubs and herbaceous species, but probably was insufficient to impair locomotion (Parker et al. 1984). Snow was unimportant in 1986; it was present intermittently, and then only in trace amounts (<10 mm).

### Sampling Procedures

Goat-induced changes in composition of the browse resource were estimated based on stem densities, stem-size distributions, stem-size—production relations, sprout abundance and weight, and utilization levels which were sampled each year prior to the trials. Herbaceous forage abundance was estimated by clipping plots. Methodological details regarding this aspect of the study have been published previously (Riggs and Urness 1989).

Response of wintering deer were estimated using tame deer which were confined to the 6 experimental pastures. With one exception, these were adults that had been reared at the Utah Division of Wildlife Resources pens in Logan and used in other experiments (Olson-Rutz and Urness 1987). The exception was a yearling female acquired from a private party in October, 1986. They were acclimated to pasture forage by ad libitum feeding of cut browse in a nearby holding facility for 10 days before their release into the experimental pastures. No data were collected for an additional 3 days to insure acclimation to the experimental setting. Dietary supplements were not offered. Twelve deer were used in 1985 (2 per pasture) during a 2-week period beginning on 29 November. Work was terminated on 14 December because unusually heavy snow made continuation of the experiment pointless. In 1986, 6 deer were used (1 per pasture) for a 7-week period beginning on 13 November. Fewer animals were used in 1986 because 5 animals died the previous summer.

Diet composition was estimated during feeding bouts that began when a deer arose from its bed to begin feeding. Data were collected for the first 60 minutes of the bout unless the animal quit feeding and returned to bedding or was distracted by external factors. Diet composition was calculated from bite counts and estimated dry weights of individual bites. Weights of bites composed of the current year's shrub leaders were predicted using twig diameter—dry-weight regressions. All other bite weights were estimated via bite simulation (Neff 1974). Twig calibrations were secured during the course of feeding bouts, and simulated bites were collected immediately thereafter.

We attempted to compare selectivity for herbaceous items based on apparent quality. Herbaceous material was classified into 3 categories based on the phenology of material in each bite taken: all green regrowth, all senescent, and mixed. Therefore, we could estimate the proportion of dietary dry matter that was consumed as bites consisting solely of green regrowth, as well as the proportion consumed as bites consisting solely of senescent material, but we were unable to account for any green material that was consumed in bites consisting of phenologically mixed material. We assumed, that if prior goat use substantially affected selection for green regrowth by deer, the effect would be reflected in the bites that consisted solely of regrowth; deer in the goat-browsed pastures would likely consume more of their dietary dry matter in bites consisting solely of regrowth.

Nutritional analyses were performed on feed samples compounded from representative plant parts taken by deer in each pasture. These were freeze-dried, ground through a 1-mm screen, and mixed according to dry-weight composition estimated for each sample bout. Neutral detergent solubles (NDS) and neutral detergent fiber (NDF) were determined using microdigestion procedures (Holechek and Vavra 1982). Aliquots were assayed for lignin and cutin (LC) content via sequential treatment with  $\text{KMnO}_4$  and  $\text{H}_2\text{SO}_4$  (Goering and Van Soest 1970). Silica (S) content was

assayed following Van Soest and Jones (1968). Crude protein (CP = nitrogen  $\times$  6.25) was determined colorimetrically (Hach et al. 1985). Protein precipitation capacity (PPC) of tannins was estimated via bovine serum albumen precipitation (BSAP) as described by Martin and Martin (1983). Digestible protein reduction (DPR) and digestible protein (DP) were calculated as described by Robbins et al. (1987a). Finally, digestibility coefficients were calculated for cell solubles (CSD), cell walls (CWD), and total dry matter (DMD) using NDS, NDF, LC, S, and DPR (Robbins et al. 1987b).

Activity budgets were estimated in 1985 via 5-minute visual scan samples (Altmann 1974) collected over a 24-hour period beginning at 0700 hours on 10 December. In 1986, the budgets were estimated from pulse-rates of leg-mounted, motion-sensitive radio transmitters<sup>1</sup>. The receiving system consisted of 2, 5-element antennae, a receiver with scanner/programmer, a digital data processor, and a dual channel strip-chart recorder. The receiving system scanned the transmitters, in rotation, for 137 seconds (2 min., 17 seconds) each; thus 822 seconds (13 min., 42 seconds) were required to scan all 6 animals, and each animal was scanned 105 times during a 24-hour sample.

Both sampling techniques employed the same activity-classification scheme. Activity discrimination was limited to inactive (i.e., lying down), moderately active (i.e., standing still or feeding), or highly active (i.e., walking, pacing, or running). Telemetry data were classified as follows: inactivity included anything done while lying down; moderate activity included any standing activity identified by a step rate  $\leq$  8 steps per minute; highly active states were associated with more than 8 steps per minute. The accuracy of telemetered observations (% correct based on a random sample of 532 validations) were as follows: 100% (inactive), 98.5% (moderate activity), 66.6% (highly active). Accuracy of visual scan samples collected in 1985 was virtually 100% for all activity states.

Moderate activity was considered representative of feeding time. We did not observe animals ruminating in the standing position; Smith et al. (1979) made similar observations. Therefore, the likelihood of confusing feeding activity with standing rumination was thought to be low. Standing idle behavior was the only other activity state that could be confused with feeding. Standing idle was almost always a manifestation of alarm, and this was rare. Also, because of the close proximity of pastures to one another, alarm tended to occur simultaneously among animals in response to common stimuli. Therefore, idle standing behavior was assumed to be unimportant as a confounding factor as well.

Foraging behavior was quantified for each sample bout in terms of travel speed ( $\text{m} \cdot \text{min}^{-1}$ ), bite rate ( $\text{bites} \cdot \text{min}^{-1}$ ), bite size ( $\text{g dry matter} \cdot \text{bite}^{-1}$ , averaged over all items taken), and projected intake rate ( $\text{g dry matter} \cdot \text{min}^{-1}$ ).

### Analysis and Experimental Design

Data were analyzed in 2 stages. First, separate analyses of treatment effects were conducted for each year's data. The experimental design was a randomized complete block in which blocks and treatment were random and fixed, respectively. The experimental unit was the pasture. This analysis was conducted separately for each year because the nature of samples and subsamples differed between years. In 1985, the deer and bouts were samples and subsamples, respectively, within the experimental units. However, in 1986 the bouts constituted samples, rather than subsamples, because there was only 1 deer per pasture.

The second analytical stage involved examining year differences, as a repeated measure, and any treatment  $\times$  year interactions (i.e., snow-dependent treatment effects). The block design was retained for this analysis, with treatment and year each considered fixed.

<sup>1</sup>MOD-400, manufactured by Telonics Inc., Mesa, Arizona.

Data were entered into this analysis at the level of the pasture means, thereby masking the annual difference in the nature of the samples.

Least-squares procedures (Bryce 1980) were used. The 1985 data set was balanced; 2 bout samples and 1 activity budget were collected for each of the 12 deer. In 1986, the number of diet samples ranged from 21 to 25 per deer. The number of electronically sampled activity budgets was 20 per deer, but not all samples were successfully completed for various technical reasons, and the number available for analysis ranged from 0 to 18 per deer. Differences among pasture means were examined for significance using Fisher's LSD (Dowdy and Wearden 1983). Unless stated otherwise, differences discussed in this paper are significant at the  $P \leq 0.05$  probability level.

## Results and Discussion

### Effects of Goats on the Winter Forage Base

Detailed descriptions of the site, its initial vegetation, and the effects of goat browsing on composition and production have been published elsewhere (Riggs et al. 1988, Riggs and Urness 1989). Goats had 3 major effects on the forage base available to wintering deer (Table 1). First, they reduced the availability of deciduous

Table 1. Approximate amounts of forage available (kg/ha) to mule deer in control pastures and treated (i.e., goat-browsed) pastures, winter 1985 and 86.

	1985 (with snow)		1986 (no snow)	
	Control	Treated	Control	Treated
Shrubs <sup>1</sup>	624	691	619	720
<i>Amelanchier alnifolia</i>	5	1	5	2
<i>Artemisia tridentata</i>	236	494	236	494
<i>Chrysothamnus viscidiflorus</i>	132	132	106	128
<i>Purshia tridentata</i>	25	3	46	3
<i>Quercus gambelii</i>	196	43	196	62
<i>Symphoricarpos oreophilus</i>	30	18	30	30
Grasses	*2	*	420	660
Forbs	*	*	9	11
Total Forage	624	691	1048	1391

<sup>1</sup>Values for *Artemisia* and *Chrysothamnus* include leaf and woody twig whereas values for the other species include only twig material.

<sup>2</sup>Asterisks indicate that snow rendered understories virtually unavailable in 1985.

browse, especially that of Gambel oak. Effects of serviceberry (*Amelanchier alnifolia* Nutt.), Douglas rabbitbrush (*Chrysothamnus viscidiflorus lanceolatus* (Hook.) Nutt.), snowberry (*Symphoricarpos oreophilus* Gray), and bitterbrush (*Purshia tridentata* Pursh.) were minor in the context of total community productivity, but generally contributed to a further reduction of deciduous browse. Second, goats increased the availability of sagebrush, roughly compensating for the deciduous browse reduction. Third, understory production, composed primarily of Kentucky bluegrass (*Poa pratensis* L.) was also enhanced.

### Diet Composition

Purely generalist foraging habits (Nudds 1980, Shank 1982) would cause deer to respond to the forage-base changes described above by markedly increasing their consumption of sagebrush relative to deciduous browse. However, purely generalist behavior is usually modified by structural characteristics of the forage base (Kenney and Black 1984a, 1984b; Black and Kenney 1984), nutrient concentrations (Belovsky 1981), and chemical deterrents (Provenza and Malechek 1984). Sagebrush, although nutritious, tends to be relatively unpalatable (Kufeld et al. 1981, Welch 1983). Therefore, deer might be expected to respond differently in this study, depending on the availability of more palatable foods.

In 1985, diets of all animals were browse-dominated because

Table 2. Effects of pasture treatment (C = control, T = browsed by goats) on botanical composition (%) of winter-time deer diets, 1985 and 1986.<sup>1</sup>

Forage Class Species	1985 (with snow)			1986 (no snow)		
	C	T	$\bar{X}$	C	T	$\bar{X}$
Shrubs	97.4	93.8	95.6 a	73.6	37.3	55.5 b
<i>Amelanchier alnifolia</i>	0.2	0.0	0.1 a	0.6	0.0	0.3 a
<i>Artemisia tridentata</i>	19.7 *	63.4	41.6 a	15.8	10.2	13.0 b
<i>Chrysothamnus viscidiflorus</i>	0.2 *	2.1	1.2 a	4.1	5.5	4.8 a
<i>Purshia tridentata</i>	15.1 *	0.2	7.7 a	24.7	2.4	13.5 a
<i>Quercus gambelii</i>	53.9 *	14.9	34.4 a	25.5	15.2	20.3 b
<i>Symphoricarpos oreophilus</i>	6.6	13.0	9.8 a	2.6	3.2	2.9 a
Other	0.0	0.0	0.0 a	0.2	1.0	0.6 b
Grasses	2.2	4.6	3.4 a	25.7	61.1	43.4 b
Forbs	0.0	0.1	0.1 a	0.5	1.5	1.0 a

<sup>1</sup>Asterisks denote significant treatment effects within a given year. Unlike letters denote significant differences between annual means.

snow cover precluded understory use, and consumption of 4 shrubs differed due to goat-induced changes in their availability (Table 2). Goats reduced availability of both bitterbrush and Gambel oak. Consequently, deer confined to the goat-browsed pastures included smaller proportions of these species, and greater proportions of sagebrush and rabbitbrush, in their diets. Diet composition did not differ between treatments in 1986.

Snow had several effects on diet composition. Most obvious was a shift from browse, to grass, in the absence of snow. Use of sagebrush and oak declined in the absence of snow while use of Oregon grape (*Berberis repens* Lindl.), a low-growing evergreen, increased. There was also the interaction between snow and goats on use of sagebrush; deer in goat-browsed pastures consumed more sagebrush than did deer in the controls, but only when snow precluded use of the understory in 1985 (Table 2). Smith et al. (1979) made similar observations.

In 1985, 97% (SE = 2) of the deciduous browse consumed was current year's growth (CYG); all the rabbitbrush consumed was CYG. Only when consuming sagebrush did animals select more substantial amounts of old woody material (13% old material in the control pastures compared to 6% in goat-browsed pastures;  $LSD_{0.05} = 16$ ). In 1986, when snow did not preclude use of the understory, all browse consumed was CYG.

Only senescent herbage extended above snow in the 1985; fall regrowth was unavailable and deer consumed only senescent material. In 1986, substantial herbage was available and consumed in all pastures. There was no evidence, however, for a consistent treatment effect on selection of regrowth. Across all pastures, 88% (SE = 2) of the grass taken was consumed in bites that consisted solely of senescent material; 10% (SE = 2) was taken as phenologically mixed material; and only 2% (SE = 0.6) was taken in bites consisting solely of regrowth. Similarly, there was no treatment effect on phenology of the forbs taken; approximately 18% (SE = 5) of the forb dry matter consumed was fall regrowth and the remainder was senescent. A significant treatment effect on consumption of all-green material (grass and forb) was seen in only 1 of the 6 pastures. In block #2, the deer in the goat-browsed pasture consumed 6% of its diet in bites consisting solely of regrowth whereas the deer in the corresponding control did not consume any regrowth. None of the other deer consumed as much as 2% of their diets in bites consisting solely of regrowth. Therefore, there was no apparent residual effect of goats on winter-time phenology of herbaceous species, and subsequent selection of high quality herbage by deer.

### Nutritional Aspects

A significant treatment effect was detected for only 1 fraction under the snow-covered conditions of 1985 (Table 3). Digestible

**Table 3. Effects of pasture treatment (C = control, T = browsed by goats) on dietary fiber fractions and digestibility coefficients, 1985-86<sup>1</sup>.**

Nutritional Parameter	1985 (with snow)			1986 (no snow)		
	C	T	$\bar{X}$	C	T	$\bar{X}$
<b>Dry-Matter Fractions<sup>2</sup></b>						
NDS	39.3	47.2	43.2 a	41.1	39.7	40.4 a
NDF	60.7	52.8	56.7 a	58.9	60.3	59.6 a
LC	26.9	29.8	28.3 a	24.0	16.4	20.2 b
S	0.5	0.4	0.4 a	1.3	2.7	2.0 b
CP	5.1	5.4	5.3 a	6.2	7.4	6.8 b
DPR	1.2 *	0.5	0.9 a	1.1	0.3	0.7 a
<b>Digestion Coefficients<sup>3</sup></b>						
CSD	20.5	30.8	25.6 a	22.8	23.0	23.1 a
CWD	16.0	14.6	15.3 a	16.9	23.0	20.0 a
DMD	36.6 *	45.4	41.0 a	39.7	46.6	43.1 a

<sup>1</sup>Asterisks denote significant differences within years. Unlike letters denote differences between annual means.

<sup>2</sup>Values for neutral detergent solubles (NDS), neutral detergent fiber (NDF), silica (S), and crude protein (CP), are expressed in terms of dry matter percentage. Lignin and cutin content (LC) is expressed in terms of NDF percentage. Digestible protein reduction (DPR) is expressed in terms of g • 100 g feed.

<sup>3</sup>Cell soluble digestibility (CSD), cell wall digestibility (CWD), and digestibility of total dry matter (DMD), in percent.

protein reduction was lower for diets consumed by deer in goat-browsed pastures than for those consumed by deer in the controls. Crude protein content was not affected by treatment, but the lower DPR for diets of treatment-confined deer meant that the digestible protein (DP) content of their diets would be higher. Still, predictions of DP were very low for diets consumed under both treatment conditions: -0.2% for diets of control deer versus +0.5% for diets of deer in goat-browsed pastures (LSD<sub>0.05</sub> = 0.6), and neither value differed significantly from zero. No treatment effects were detected for NDS, NDF, LC, or S. Digestibility coefficients for cell solubles or cell walls did not differ between treatments in 1985. However, a treatment effect was indicated for total dry matter digestibility ( $P = 0.07$ ) which was presumably a cumulative effect of less marked differences in the individual fiber and protein fractions. The apparent improvement should be balanced, however, by recognizing that the ultimate value of food is determined by both the net and metabolizable coefficients, in addition to the digestibility coefficient. We estimated only digestibility.

Prior goat use did not significantly affect any nutritional fraction or digestibility coefficient in the snow-free winter of 1986. Digestible protein averaged only 2.2 g • 100g<sup>-1</sup> feed across the 6 animals (SE = 0.4). The lowest DP value was calculated for the deer confined to control pastures in block #2 (-1.4%); its diet consisted almost solely of deciduous browse. The highest value was calculated for the deer confined to the goat-browsed pasture in that same block (+4.0%); its diet was mostly grass, and it was the only animal that apparently selected fall regrowth to a significant degree.

These observations indicate that any significant improvement of dietary quality under snow-free conditions depends primarily on management of the herbaceous understory, and not on browse management. Senescent herbage eaten by wintering deer is generally of poor quality (Bartmann 1983), and it can only be expected to decline in quality as winter progresses (Demarchi 1968). Most herbage selected under snow-free conditions in this study was senescent because the pastures were rested during the summer of 1986, allowing plant phenology to progress unabated. Consequently, fall regrowth was largely obscured by the taller, senescent material. Deer did not effectively select for the more nutritious regrowth, and their diet quality suffered; this was predictable based on earlier works (Arnold 1964, Willms et al. 1979, Smith et al.

1979). This condition is probably representative of what would occur in years following a goat treatment if the pasture was protected from further grazing. Wickstrom et al. (1984) demonstrated that the ability of mule deer to harvest dry matter is relatively insensitive to declining standing crop. These results show that the ability to select high-quality dry matter in winter can be impaired at relatively high standing crops, even under snow-free conditions when some regrowth is available. Annual grazing by cattle or sheep in summer would probably improve the ability of deer to select a high-quality diet in this situation (Smith et al. 1979, Willms et al. 1979, but see Austin et al. 1983). Relative effectiveness of different grazing programs cannot be predicted because effects on sward structure, available biomass, and green:dead ratios, as well as the subsequent interrelated effects of these on diet selection remain unquantified generally.

Lignin and cutin, S, and CP each differed between years without respect to treatment (i.e., as a function of snow). Lignin and cutin contents were greater in 1985 than in 1986. This was expected on the basis of the shift away from browse that occurred in the snow-free year (Robbins 1983). Silica was considerably greater in 1986 than in 1985. This was also expected based on the shift toward grass in 1986, most of which was senescent. However, the magnitude of the difference should be viewed with caution because of possible soil contamination in the hand-plucked herbage samples of 1986. As a result, 1986 DMD estimates may be somewhat negatively biased. Dietary CP was higher in 1986 as well.

There was a treatment × year interaction for CWD (Table 3); CWD was higher in treated pastures, but only under snow-free conditions. Dietary habits driving the difference were probably increased consumption of understory plants, some of which were phenologically young, and reduced consumption of previous years' browse growth. There was also a significant interaction effect on DMD. Digestibility of diets consumed by deer in the goat-browsed pastures was higher than that of diets consumed by deer in the controls, but the difference was significant only in 1985.

#### Activity Budgeting and Foraging Behavior

We anticipated that energetic expenditures would change as a result of the goat-induced changes in the forage base. Differences in the way animals budgeted their time could conceivably intensify the effects of nutritional differences on energy balance. For example, forage quality could affect energy expenditures by regulating feeding time. Rumination time per gram of ingesta increases with cell wall content of feed (Van Soest 1982), and feeding time might be limited by slow passage rates when consuming high-fiber feeds. Risenhoover (1986) suggested that winter foraging time of Alaskan moose is so limited. Mule deer might similarly have their feeding time constrained due to extended rumination when feeding on high-fiber forage such as deciduous browse or senescent grass. Conversely, consumption of lower-fiber diets (e.g., sagebrush or herbaceous regrowth) might reduce rumination time and allow greater feeding time, assuming the latter is regulated by gut-fill.

Activity budgets, however, did not differ significantly between treatments or years. These animals were apparently less active than those studied by Kufeld et al. (1988). Animals in all pastures partitioned their time similarly. They spent most of their time lying down (66.5%, SE = 1.3), followed by moderate (31.7%, SE = 1.2) and highly active (1.8%, SE = 0.6) states, respectively.

Moreover, differences were not predicted based on either the environmental conditions or nutrition. Temperatures were similar between years, and the coldest temperature recorded in either year was -18° C, which is above the estimated lower critical temperature for a standing adult (Parker and Robbins 1985). Furthermore, snow depth in 1985 was probably not sufficient to restrict movement based on estimates by Parker et al. (1984). Therefore, there was no particular reason to expect activity budgets to differ signifi-

cantly between years as an energy conserving response to climatic differences. Regarding nutrition, dietary NDF did not differ significantly between treatments or years, although the LC component of NDF was higher in 1985 due to the higher browse consumption. However, this difference was probably not great enough to alter passage rates sufficiently to be reflected in activity patterns, at least with the resolution possible in our sampling scheme.

Foraging efficiency can also respond to forage-base changes, and conceivably affect activity. Search effort, for example, could increase in response to a decline in the density of acceptable forage. This, in turn, could be expressed in increased travel rates (Collins et al. 1978, Wickstrom et al. 1984). Bite size and bite rate could be affected by changes in acceptable forage availability. However, these 2 variables interact in a strong inverse-curvilinear manner to compensate for one another over a broad range of foraging conditions (Wickstrom et al. 1984). More important is identification of the lowest availability at which this interaction is no longer compensatory. Below this point, intake rate, and hence feeding time, could be adversely affected, thereby affecting habitat selection as well (Collins and Urness 1983).

Treatment-related differences in projected intake rate would be indicative of a reduction of acceptable forage availability to a biologically significant level, and a difference was anticipated between treatments in this study based on the low palatability of sagebrush. However, no treatment effect was detected for any foraging variable in either 1985 or 1986 (Table 4). Therefore, we con-

**Table 4.** Summary of treatment (C = control, T = goat-browsed) effects on foraging behavior, 1985 and 1986.<sup>1</sup>

Variable	1985 (with snow)			1986 (no snow)		
	C	T	$\bar{X}$	C	T	$\bar{X}$
Travel rate, m • min <sup>-1</sup>	5.0	6.7	5.9 a	1.8	1.4	1.6 b
Bite Rate, bites 1 • min <sup>-1</sup>	3.6	2.1	2.9 a	12.6	10.9	11.8 b
Bite Size, g • bite <sup>-1</sup>	0.2	0.2	0.2 a	0.1	0.1	0.1 a
Intake rate, g • min <sup>-1</sup>	0.7	0.5	0.6 a	1.6	1.2	1.4 b

<sup>1</sup>Treatment effects not significant in either 1985 or 1986 ( $P \leq 0.10$ ). Unlike letters denote differences between annual means ( $P \leq 0.05$ ).

cluded that goat-induced vegetal changes did not substantially impact acceptable-forage density in either year. Of greater interest were differences that did occur between years without respect to treatment. The animals moved more rapidly, and had lower bite rates and projected intake rates, in 1985 than in 1986. Bite size did not differ between years. Thus snow cover apparently lowered the density of acceptable food times, and prompted less efficient foraging as reflected by intake and travel rates. However, the decrease in foraging efficiency did not extend feeding time, as reflected by moderate activity.

This suggests that daily intake of digestible dry matter was substantially less in 1985 than in 1986, assuming that deer did not compensate during feeding periods we did not sample and that our bite estimates were reasonably accurate. These are reasonable assumptions in our view. The relatively small differences in nutritional quality argue against a passage-rate bottleneck. The activity-budget sample size may not have been sufficient to detect an effect, but we believe this is unlikely because the conditions were quite consistent throughout the sample period.

Alternatively, intake may not have been limited by gut-fill in 1985; deer may simply limit intake because of low browse palatability. If so, the question remains whether this behavior is representative. In terms of foraging habits, these particular deer were found to be generally representative of wild animals in spring, summer, and fall (Olsen-Rutz and Urness 1987); however, they were not compared to wild deer in winter. Forage palatability and options

can decrease markedly under snow-covered conditions. It is still possible that the lower intake rate observed under snow-covered conditions was an artifact of using tame animals. We attempted to guard against this via the lengthy acclimation period, but we cannot demonstrate that we were successful. If the behavior was indeed representative, the negative effects of snow on energy balance in this situation were likely mediated through both increased foraging costs and decreased intake. However if the behavior was not representative, negative effects of snow were likely mediated through foraging costs alone.

## Conclusions

We found that under snow-covered winter conditions deer responded to goat-induced vegetal changes by increasing the proportion of sagebrush in their diets, thereby enhancing dry matter digestibility, but not available protein content. The beneficial effect was absent under snow-free conditions because animals grazed grasses and forbs, presumably because of the lower relative palatability of sagebrush. Dietary digestibility was not significantly better under snow-free conditions than it was under snow-covered conditions. This occurred largely because the availability of herbaceous regrowth was not substantially affected. Finally, energy expenditures of wintering deer were not markedly affected by goat-induced vegetal changes, regardless of snow conditions.

Periodic goat-browsing can be a practical means of managing successional trajectory and composition of oakbrush winter range. Mass-specific quality of winter-time deer diets can be augmented to some extent under snow-covered conditions as a result. However, this apparent positive effect may be negated to some degree if deer reduce intake because of the low palatability of sagebrush; conversion to superior varieties of sagebrush may provide a long-term solution to this problem (Welch et al. 1981). If high dietary quality is to be attained under snow-free conditions, particularly in terms of digestible protein, annual manipulation of the understory is required as well. Snow cover is intermittent on many oakbrush-dominated sites. Where this occurs, the nutritional plane of wintering deer can be more responsive to understory management than to shrub management, depending on the frequency and duration of snow cover.

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