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Dietary Partitioning of Toxic Leaves and Fibrous Stems Differs Between Sympatric Specialist and Generalist Mammalian Herbivores

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Dietary specialists often reside in habitats that provide a high and predictable abundance of their primary food, which is usually difficult for other herbivores to consume because of high levels of plant toxins or structural impediments. Therefore, sympatric specialist and generalist herbivores may partition food resources within and among plants. We compared how a dietary specialist (pygmy rabbit, *Brachylagus idahoensis*) and generalist (mountain cottontail, *Sylvilagus nuttallii*) used sagebrush as a food resource during winter across 3 field sites in Idaho, USA, and in controlled feeding trials with captive rabbits. The proportion of sagebrush consumed by both rabbit species varied among sites, indicating that characteristics of sagebrush plants and the surrounding plant community influenced use of sagebrush. In addition, free-ranging and captive pygmy rabbits consumed a greater proportion of sagebrush and cropped smaller stem diameters with a greater proportion of sagebrush leaves (high monoterpenes, low fiber) relative to stems (low monoterpenes, high fiber) than did cottontails. Cottontails frequently discarded the leafy tips of sagebrush branches. Cottontails are more tolerant of fiber and less tolerant of sagebrush toxins than pygmy rabbits. Cottontails consumed large diameter stems, which diluted toxins in sagebrush but increased fiber intake and reduced digestible nitrogen intake. Pygmy rabbits are less tolerant of fiber but more able to detoxify and eliminate sagebrush toxins than cottontails. Pygmy rabbits consumed small diameter stems, which reduced fiber intake, but increased intake of toxins from sagebrush leaves. Although partitioning of stems and leaves within sagebrush plants may provide a mechanism for coexistence of specialist and generalist rabbits, higher than expected dietary overlap between both free-ranging and captive rabbits in winter might create resource competition in areas with high-density sympatric populations or low availability of sagebrush. In addition, these contrasting foraging strategies have the potential to influence dynamics of sagebrush communities over time.

Keywords: *Brachylagus idahoensis*, coexistence, competition, fiber, mountain cottontail, plant secondary metabolites, pygmy rabbit, *Sylvilagus nuttallii*

Less than 1% (~20) of all mammal species are considered dietary specialists that consume a narrow diet of only 1 type of plant (Dearing et al. 2000; Shipley et al. 2009). Specialization requires exceptional physiological and behavioral mechanisms to more efficiently extract required energy and nutrients from one particular plant type. However, specialization comes at the potential loss of dietary and habitat flexibility. Therefore, the plants consumed by dietary specialists usually have 2 main characteristics. First, to reduce competition with dietary generalists, specialist herbivores must focus on plants that are intrinsically "difficult" for most herbivores to consume because they contain high levels of plant secondary metabolites (PSMs), plant fiber, or unusual physical obstructions (Robinson and Wilson 1998; Dearing et al. 2000; Shipley et al. 2009; Kohl et al. 2016). PSMs such as terpenes, alkaloids, and phenolics are "difficult" because they impose a physiological cost that reduces the nutritional value of the food or could end in toxicosis or death as they are absorbed, metabolized, and excreted by the animal (Freeland and Janzen 1974; Sorensen et al. 2005; Torregrossa and Dearing 2009; Shipley et al. 2012). Plants with high levels of fiber are "difficult" because fiber dilutes energy and nutrients, reducing the extent and rate at which nutrients can be extracted from food (i.e., Hoover and Heitmann 1972; Van Soest 1994; Iason and Van Wieren 1999).

Second, because of their reduced dietary breadth and flexibility, specialists must consume a plant type that occurs in high and predictable abundance year-round (Westoby 1978; Crawley 1983; Shipley et al. 2009). For example, most mammalian herbivores that are considered specialists, such as many arboreal marsupials (e.g., koalas, *Phascolarctos cinereus*; common ringtail possums, *Pseudocheirus peregrinus;* Moore et al. 2005; Marsh et al. 2003), tree squirrels (e.g., Abert's squirrels, *Sciurus aberti*; woolly flying squirrels, *Eupetaurus cinereus*; Zahler and Kahn 2003; Murphy and Linhart 1999), and woodrats (e.g., *Neotoma stephensi, N. lepida*; Dial 1988; McEachern et al. 2006), consume a monospecific or monogeneric diet of evergreen trees like *Eucalyptus* spp. or conifers (e.g., *Pinus* spp.; *Juniperus* spp.). Although the foliage of these trees contains high levels of PSMs, it also provides relatively consistent levels of nutrients year-round, and these trees often grow relatively uniformly across large landscapes (Snyder and Linhart 1998; Youngentob et al. 2012).

Although specialist herbivores are usually restricted to habitats that provide plants that meet those criteria, generalist herbivores have wide dietary niches and often use those habitats sympatrically with specialists. Because generalists typically have a reduced ability to detoxify specific PSMs or consume other difficult foods, they are expected to consume smaller amounts of the specialist's primary food by mixing their diets with less difficult foods or selecting plant parts that are less difficult (Freeland and Janzen 1974; Sorensen and Dearing 2003; Marsh et al. 2006). These differences might effectively allow the specialist and generalist to reduce competition by partitioning food resources in shared habitats. For example, arboreal marsupials roughly partition food resources based on subgenera of *Eucalyptus* (i.e., *Symphyomytus* and *Monocalyptus*) and by the type of PSMs in the plant (Jensen et al. 2014), sympatric specialist and generalist woodrats partition diets within the Great Basin desert (Dial 1988), and sympatric bamboo lemurs (*Hapalemur griseus, H. aureus, H. simus*) tend to use different parts of the fibrous bamboo plant (Glander et al. 1989; Tan 1999). Furthermore, sympatric generalists and specialists may actually benefit each other through feeding facilitation (Arsenault and Owen-Smith 2002). For example, in the Serengeti of Tanzania, heavy grazing by migrating wildebeest (*Connochaetes taurinus*) promotes regrowth and increased nutrient content and digestibility of forage that benefits the smaller Thomson's gazelles (*Eudorcas thomsonii*; McNaughton 1976). However, little information exists within communities of specialist and generalist mammals about the extent of competition, resource partitioning, and facilitation. A better understanding of how sympatric specialist and generalist herbivores use abundant but difficult forage resources would help elucidate community structure, adaptations for consuming difficult foods, potential competition for food resources, and dietary tradeoffs when selecting plants or plant parts based on physiological tolerance to difficult characteristics of plants.

Sagebrush, which covers 25 million ha in western North America, is an example of a difficult forage that often grows abundantly across large steppe landscapes. Because it is evergreen and its leaves are nutritious (i.e., relatively high in dry matter digestibility and crude protein; Kelsey et al. 1982; Shipley et al. 2006; Ulappa et al. 2014), it can provide a stable food source for herbivores year-round. However, sagebrush also contains high levels of monoterpenes and other PSMs that deter most foragers from including substantial amounts in their diets (Kelsey et al. 1982; Dearing et al. 2000; Iason and Villalba 2006). Not surprisingly, sagebrush-steppe is shared by a vertebrate community consisting of only a few specialists consuming high amounts of sagebrush year-round (e.g., pygmy rabbits [*Brachylagus idahoensis*] and greater sage-grouse [*Centrocarpus urophasianus*]), and a suite of generalists that eat at least a small amount of sagebrush, especially in winter when the understory of grass and forbs are senescent or covered with snow. In particular, pygmy rabbits often share habitats with another leporid, the generalist mountain cottontail (*Sylvilagus nuttalli*; Orr 1940; Chapman 1975; Green and Flinders 1980a; MacCracken and Hansen 1982) where their competition for food is thought to be minimal (Johnson and Hansen 1979; MacCracken and Hansen 1984). However, little is known about the extent to which free-ranging mountain cottontails use sagebrush for food, especially where sympatric with pygmy rabbits.

Like other dietary specialists, pygmy rabbits are better able to tolerate the PSMs in sagebrush than their generalist counterparts (Shipley et al. 2012), whereas cottontails are able to digest plant fiber to a greater extent than pygmy rabbits (Shipley et al. 2006). As a consequence, when given a choice, captive pygmy rabbits chose to consume higher levels of sagebrush PSMs to avoid consuming higher-fiber foods, whereas mountain cottontails chose to consume higher-fiber food to avoid consuming sagebrush PSMs (Camp et al. 2015). Therefore, our goal was to examine how these dietary tradeoffs might extend to dietary partitioning of food resources by specialist and generalist rabbits foraging sympatrically in natural sagebrush habitats. The tradeoff between minimizing PSMs and maximizing digestible energy and protein has been suggested to govern stem diameters selected by other generalist herbivores such as snowshoe and mountain hares (*Lepus americanus*, *L. timidus;* Bryant et al. 1992; Palo et al. 1992) and moose (*Alces alces*; Shipley et al. 1998; Stolter et al. 2005). Therefore, generalist and specialist herbivores might make different tradeoffs between PSMs and plant fiber not only when selecting which plants to eat, but when selecting plant parts from individual shrubs or trees.

To test how differences in foraging strategies might provide a mechanism for coexistence of pygmy rabbits and cottontails, we first determined the mass of leaves and stems, and concentration of plant fiber, digestible protein, and monoterpenes of sagebrush leaves and sagebrush stems cut at increasing stem diameters. We used these parameters to develop predictive curves depicting the dry mass, proportion of leaves and stems, and nutritional value of sagebrush at different stem diameters. We then compared pygmy rabbits and cottontails in 3 experiments: 1) amount of sagebrush, proportion of leaves and stems consumed, and stem diameters cropped by sympatric free-ranging pygmy rabbits and cottontails in 3 sagebrush steppe landscapes during the winter, 2) proportion of sagebrush leaves and stems consumed and stem diameters cropped by captive pygmy rabbits and cottontails at 2 levels of food supplementation, and 3) differences between use of sagebrush by free-ranging and captive rabbits. We predicted that sagebrush leaves would have a higher concentration of monoterpenes and digestible protein, and a lower concentration of fiber, than would stems, and that monoterpene and digestible protein concentration would decline with increasing stem diameter, as is common in other woody plants (Palo et al. 1992; Spaeth et al. 2002; Wilson and Kerley 2003). Second, given the higher tolerance to PSMs and lower tolerance to fiber by pygmy rabbits compared to cottontails (Shipley et al. 2006, 2012), we predicted that pygmy rabbits would trade off fiber for PSMs by consuming more sagebrush, a greater proportion of sagebrush leaves versus stems, and a smaller stem diameter than would cottontails. We expected that when more alternative, high-quality food was available, both rabbit species would consume a lower proportion of sagebrush and a greater proportion of stems because they might not need the additional nutrients from the more toxic leaves.

Materials and Methods

Study areas.— We conducted the field portion of this study at 3 field sites in Idaho, USA; 2 sites were located about 6 km apart in the Lemhi Valley along the eastern border of the state (i.e., Cedar Gulch and Rocky Canyon), and 1 site was located near Fairfield in south-central Idaho, USA (i.e., Magic Reservoir). All 3 field sites were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and mima mounds, which are microtopographic, taller mounds of deeper soils that usually support taller, denser sagebrush than the surrounding area. Cedar Gulch (-113.28444°, 44.69733°; elevation: 1880-1925 m) also had black sagebrush (*A. nova*), rabbitbrush (*Chrysothamnus* spp.), grasses, and forbs. Rocky Canyon (-113.22252°, 44.66059°; elevation: 1,950-2,125 m) is co-dominated by Wyoming big sagebrush and three-tip sagebrush (*A. tripartita*) but also included black sagebrush, rabbitbrush, grasses, and forbs. Magic Reservoir (-113.471914°, 40.437746°; elevation: 1,470 m) also had low sagebrush (*A. arbuscula*), three-tip sagebrush, grasses, and forbs.

Dietary quality of sagebrush.— Wyoming big sagebrush used for analyses of dietary quality was collected from 5 distinct areas with 30-m radii, both on and off mima mounds, near the Cedar Gulch study site in January 2015. At each area, 2 – 5 branches were clipped from each of 50 – 100 sagebrush plants with pruning shears and frozen immediately to prevent sample degradation. In the laboratory, branches were re-cut at 1-, 3-, and 5-mm diameter to yield 3 groups that were frozen with dry ice to separate leaves and stems using a rubber mallet. Each group of leaves or stems at each diameter was then ground to pass a 1-mm screen.

We measured the neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), and acid-insoluble ash (AIA) content of duplicate composite samples of sagebrush leaves and stems cut at each diameter (Goering and Van Soest 1970; Mould and Robbins 1981) with filter bags, sodium sulfite, and alpha amylase using an Ankom Fiber Analyzer$^{200/220®}$ (Ankom Technology, Fairport, New York). We determined nitrogen content (%) of all samples using a Carbon-Nitrogen TruSpec analyzer (LECO; St. Joseph, Michigan) and estimated crude protein (CP) content as 6.25 times the nitrogen content (Robbins 1993). We estimated dry matter digestibility and digestible nitrogen from the summative equations of Robbins et al. (1987a,b). Although developed for wild ungulates, these equations resulted in values consistent with digestible protein of sagebrush samples measured using in vitro approaches developed for small hindgut fermenters (DeGabriel et al. 2008; Camp 2012).

To determine the total monoterpene concentration of sagebrush leaf and stem samples at each diameter, we extracted the monoterpene essential oils by hydrodistillation for 2 h using 50 to 60 g fresh mass of each sagebrush samples composited separately for each of the 5 collection areas at Cedar Gulch. Oils were collected in a Clevenger-style water trap washed with dichloromethane solvent to ensure recovery of any solid monoterpenes and low volume oils. The solvent was removed on a roto-evaporator with vacuum at room temperature and then weighed. We report oil yield as percent of tissue dry mass calculated with fresh tissue water content measurements from triplicate subsamples (see Supplementary Data SD1 for full methods). We then determined the individual monoterpene profiles of the essential oils extracts using a gas chromatograph (GC; Agilent 6890N) with a headspace auto-sampler (Hewlett-Packard HP7694). Oils extracted (100 mg) from stems and leaves were weighed into a 20-ml gas chromatography headspace vial. Retention times and peak areas (area under the curve, AUC) of each monoterpene were calculated using Hewlett-Packard ChemStation version B.01.00 (Agilent Technologies, Santa Clara, California). Compound peaks were identified using a cocktail of known monoterpene standards (see Supplemental Data SD2, SD3) to generate reference retention times. However, not all compounds could be identified and unknown compounds were differentiated based on retention times (min). Headspace and gas chromatograph settings and operating conditions are found in Supplementary Data SD2. We compared the content of extracted oil (as a proxy for total monoterpene content) between sample type (leaves, 1-mm, 3-mm, 5-mm stems) using a 1-way analysis of variance (ANOVA; RStudio Team 2015) with collection area as the experimental unit. We compared the area ratios of different monoterpene peaks between leaf and stem oils using a 1-way ANOVA.

To determine the relationship between stem diameter cropped by rabbits and mass of tissue (i.e., total mass, mass of leaves and stems, and the proportion of dry leaf to dry stem mass), we cut 13 sagebrush samples at each stem diameter ranging from 1 – 5 mm in 0.5-mm increments from plants collected at the Cedar Gulch site. We separated leaves and stems, corrected for dry matter, and modeled dry mass of leaves, stems, and whole branches in relation to stem diameter using a power function, and the proportion of leaves relative to the total mass of the sagebrush in relation to stem diameter using a logarithmic function. We estimated the total monoterpene and digestible protein content of stems with leaves at different diameters from the predicted proportion of leaves and the measured value of these constituents.

Diets of free-ranging rabbits.— To determine the proportion of sagebrush and the proportion of leaves and stems of sagebrush consumed by free-ranging pygmy rabbits and cottontails during winter, we collected 9 – 11 groups of fecal pellets from each rabbit species at each of our 3 study sites (Cedar Gulch, Rocky Canyon, and Magic Reservoir) during January 2014. Fresh feces were collected from the top of the snow from 1 pile or along a fresh rabbit trail. Individual samples were collected ≥ 20 m apart to minimize collection from the same animal. We determined the composition of sagebrush leaves, stems, forbs, grasses, and other shrubs from the fecal samples using microhistological analyses conducted at the Wildlife Habitat Laboratory, Washington State University (WSU), Pullman, Washington. We compared the proportion of the total diet composed of sagebrush, and the proportion of sagebrush composed of leaves versus stems, between rabbit species, among study areas, and their interaction using a 2-way ANOVA.

To determine the stem diameter of sagebrush selected by free-ranging pygmy rabbits and cottontails, we identified Wyoming big sagebrush that had been browsed by pygmy rabbits and cottontails at the Cedar Gulch site during January 2016. We determined the species responsible for the browsing from crop marks severed at a 45° angle (Ulappa 2011), tracks in the snow, fecal pellets, visual confirmation, and burrows (pygmy rabbits only). We measured stem diameters of each crop mark to the nearest 0.01 mm for between 20 and 74 crop marks per shrub that could be confidently attributed to a single browser, either a pygmy rabbit or cottontail. We estimated the dry mass, proportion of sagebrush leaves, fiber content, digestible protein, and monoterpenes consumed by these free-ranging rabbits from stem diameter cropped using our models described previously. We calculated dry mass of leaves and stems consumed by multiplying dry mass of sagebrush and the proportion of leaves for each stem diameter, and then calculated the proportion leaves consumed by a single forager.

Foraging experiments with captive rabbits.— To measure tradeoffs made by pygmy rabbits and cottontails when consuming sagebrush leaves and stems in a controlled setting, we conducted 2 sagebrush feeding experiments with wild-caught pygmy rabbits and mountain cottontails at the Small Mammal Research Facility at WSU. Pygmy rabbits used in the captive studies were captured at field sites throughout their range in Idaho (Scientific Collection Permits (SCP) #100310 and #010813) and Montana (SCP #2014-062) within 1 month to 3 years before participating in the feeding trials. Because mountain cottontails are much more difficult to capture in sagebrush-steppe habitats, they were captured in the Palouse of eastern Washington (SCP #14-206). While in captivity, rabbits of both species were maintained on a basal diet of commercial rabbit pellets (Purina ® Rabbit Chow Professional, Purina Mills, LLC., St. Louis, Missouri; 36% NDF, 18% crude protein) with supplementary fresh forbs and sagebrush, and water *ad libitum*. Husbandry practices and experimental procedures were approved by the WSU Institutional Animal Use and Care Committee (SOP #4219, ASAF #4398) and followed the guidelines approved by the American Society of Mammalogists (Sikes et al. 2016).

To determine the proportion of sagebrush leaves versus stems selected by captive pygmy rabbits and cottontails, and the influence of the amount of supplementary food on this selection, we conducted 2 sets of feeding trials from January – March 2014 with 8 pygmy rabbits (431 ± 5 g; 4 males, 4 females) and 5 mountain cottontails (1,041 ± 14 g; 3 males, 2 females). During the feeding trials, rabbits were housed indoors in 0.64 × 0.64 × 0.43 m metal rabbit crates with a plastic tube for refuge. For 5 – 10 days preceding foraging experiments, rabbits were fed Wyoming big sagebrush (branches of leaves and stems) collected January 2014 near the Cedar Gulch site and kept frozen until just before feeding each day. Immediately following the experimental trials acclimation period, frozen sagebrush leaves were separated from stems using dry ice and a rubber mallet. Each day of a 3-day trial, each rabbit received a bowl of *ad libitum* sagebrush leaves, a bowl of *ad libitum* sagebrush stems cut at a 3-mm diameter (the approximate diameter of annual growth in sagebrush; Dean et al. 1981), and a bowl of the basal diet provided at 50% (Trial 1) or 25% (Trial 2) of their normal daily intake. Leaves and stems were refreshed every 12 h to prevent excessive volatilization of monoterpenes. Although we did not measure oil volatilization from sagebrush during this study, when 1,8-cineole, one of the major monoterpenes in sagebrush, was added directly to rabbit pellets, only 1% was lost over a 12-h period (Utz 2012). The volatilization rate from sagebrush plants in this study was likely even slower because the glands retain the volatiles. For example, < 5% of monoterpenes were lost from the leaves of peppermint (*Mentha piperita*) over a 6-month period (Gershenzon et al. 2000). We calculated consumption of sagebrush and basal diet by the difference between the dry mass offered and refused. We compared the proportion of the total diet composed of sagebrush, the proportion of the sagebrush composed of leaves, the dry mass of sagebrush consumed, and the total dry mass of food consumed (sagebrush + basal diet) between rabbit species, sex of rabbits, level of basal diet, day of trial, and the interaction between species and sex using a mixed effects model with individual rabbit as the random variable.

To determine the stem diameter cropped by captive pygmy rabbits and cottontails when offered intact braches of sagebrush, and the resultant proportion of sagebrush leaves they consumed, we conducted another set of feeding trials from January – March 2015 with 11 pygmy rabbits (429 ± 13 g; 5 males, 6 females) and 8 mountain cottontails (1,131 ± 24 g; 4 males, 4 females). Animals were housed individually in 2.3 × 1.25 m pens with a 120-cm long plastic tube and an insulated nest box for refuge. Because our remote cameras (Moultrie D-555i, EBSCO Industries, Inc., Calera, Alabama) and previous research (Verts and Gehman 1991; Larrucea and Brussard 2009; Lee et al. 2010) indicated that feeding peaks occur in early morning for pygmy rabbits and mountain cottontails, the trials were conducted between 2300 – 0600 h. Each rabbit only performed 1 trial, and to ensure active foraging on the sagebrush, the basal diet was removed during that period. At 2300 h, each rabbit was offered 6 branches of fresh-frozen Wyoming big sagebrush that had been collected January 2015 near the Cedar Gulch site. Each branch was cut at ≥ 3 mm diameter, ensuring a larger diameter than any individual of either rabbit species would crop in preliminary trials, and anchored to 15-mm holes 7.6-cm apart in a plywood strip using size 00 rubber stoppers (Fig. 1). To control for different branching architecture and leafiness of offered branches, sagebrush branches were grouped based on 6 differing morphologies and 1 branch from each group was offered to each rabbit (see Supplementary Data SD4). Branches were sorted categorically based on height, branching pattern, and leafiness (Fig. 1; see Supplementary Data SD4). Uneaten sagebrush was collected at 0600 h the next morning and the stem diameters of all crop marks were measured with calipers to the nearest 0.01 mm. Cottontails often cropped apical parts of the branches and discarded them uneaten, thus we also collected these refusals and measured their diameters. To estimate the mass of stems and leaves consumed by the rabbits, we first calculated the proportion of leaves and stems on 15 representative branches of each of the 6 morphologies. Before each trial, we measured the fresh mass of each branch offered, corrected it for dry matter, and estimated dry mass of stems and leaves from the average proportion in the representative branches of each morphology. After each trial, we separated and weighed the leaves and stems from the remaining branches and the discarded apical parts of the branches and estimated the mass consumed from the dry mass offered and refused.

We compared stem diameters cropped, the estimated proportion of leaves consumed between rabbit species, captivity status (free-ranging versus captive), and their interaction using a 2-way ANOVA. We compared the diameters cropped by cottontails to the diameters of the apical parts of the branches that were discarded between whether it was consumed or discarded, captivity status, and their interaction using a 2-way ANOVA. Because pygmy rabbits consumed leafier apical stems and cottontails discarded them, we compared the stem diameters and the resulting calculated proportion of leaves between species (discarded versus consumed), captivity status and their interaction using a 2-way ANOVA. Finally, we compared the calculated proportion of leaves that was discarded to the consumed proportion of leaves by captive and free-ranging cottontails.

Results

Dietary quality of sagebrush.— Sagebrush leaves and stems differed in levels of fiber, protein, and monoterpenes. NDF, ADF, and ADL were about twice as high in stems than leaves, and increased with increasing stem diameter (Table 1). In contrast, crude protein concentration was about twice as high in leaves than stems, and decreased with increasing stem diameter (Table 1). As a consequence, estimated dry matter digestibility and digestible protein content were also substantially higher in leaves than stems (Table 1). Total monoterpene content differed with plant part ($F_{3,12} = 194.10$, $P < 0.001$). Leaves contained over 6 times more total monoterpene content than 1-mm stems, and monoterpene concentration declined with increasing stem diameter (Table 1). Leaves and stems contained the same identified individual monoterpenes (i.e., β-pinene, 1,8-cineole, and camphor; Supplementary Data SD3), but in different relative amounts. Leaves had relatively more β-pinene ($F_{3,16} = 3.38$, $P = 0.04$) and 1,8-cineole ($F_{3,16} = 18.15$, $P < 0.001$) as a proportion of total monoterpenes, and also had more 1,8-cineole per unit β-pinene than did stems ($F_{3,16} = 8.28$, $P = 0.002$; Table 1). Dry mass of sagebrush leaves ($F_{1,97} = 376.89$, $P < 0.001$, $R^2 = 0.79$; Fig. 2a), stems ($F_{1,97} = 940.93$, $P < 0.001$, $R^2 = 0.91$; Fig. 2b), and both combined ($F_{1,97} = 924.40$, $P < 0.001$, $R^2 = 0.90$; Fig. 2c) increased with stem diameter. However, larger stems supported a lower proportion of leaves ($F_{1,97} = 60.88$, $P < 0.001$, $R^2 = 0.39$; Fig. 2d).

Proportion of sagebrush, stems, and leaves consumed by free-ranging and captive rabbits.— Free-ranging pygmy rabbits consumed more sagebrush and a greater proportion of leaves than cottontails, even though diets varied among study sites. The proportion of sagebrush in the feces of free-ranging rabbits differed between species ($F_{1,58} = 148.51$, $P < 0.001$) and among sites ($F_{2,57} = 21.56$, $P < 0.001$), but the species × site interaction was not significant ($F_{5,54} = 1.34$, $P = 0.27$). Pygmy rabbits ate a greater proportion of sagebrush ($\overline{X} = 0.84$, $SE = 0.05$) than did cottontails ($\overline{X} = 0.28$, $SE = 0.04$), and both species ate less sagebrush at the Magic site relative to the 2 other field sites (Fig. 3). In addition, the proportion of sagebrush leaves versus stems present in the feces also differed between rabbit species ($F_{1,58} = 36.94$, $P < 0.001$) and among sites ($F_{2,57} = 3.09$, $P = 0.05$), but the interaction was not significant ($F_{5,54} = 0.66$, $P = 0.52$). Pygmy rabbits ate a greater proportion of leaves ($\overline{X} = 0.60$, $SE = 0.03$) than did cottontails ($\overline{X} = 0.32$, $SE = 0.05$), although both species ate a greater proportion of leaves at the Cedar Gulch site than the 2 other sites (Fig. 4).

Similarly, when offered separate bowls of sagebrush leaves and stems along with their basal diet, captive pygmy rabbits also consumed more sagebrush and a greater proportion of leaves than did cottontails, even though diets varied with the percentage of basal diet offered (Table 2). The proportion of total sagebrush consumed differed between rabbit species ($F_{1,9} = 14.74$, $P = 0.004$) and with amount of basal diet offered (50% or 25%; $F_{1,63} = 539.16$, $P < 0.001$), but neither day ($F_{1,63} = 3.37$, $P = 0.10$) nor sex ($F_{1,9} = 2.17$, $P = 0.17$), nor the species × sex interaction ($F_{1,9} = 4.70$, $P = 0.06$) was significant. Sagebrush formed a greater proportion of the diet of captive pygmy rabbits than of cottontails, and the proportion of sagebrush consumed by both species was about 50% higher when less basal diet was available (Table 2). The dry mass of sagebrush consumed by captive rabbits did not differ between species ($F_{1,9} = 0.97$, $P = 0.35$) or sexes ($F_{1,9} = 1.45$, $P = 0.25$), and the species × sex interaction was not significant ($F_{1,9} = 3.92$, $P = 0.08$), but rabbits did increase intake of sagebrush when more basal diet was available ($F_{1,63} = 64.67$, $P < 0.001$; Table 2) and as the trial progressed ($F_{1,63} = 6.41$, $P = 0.01$; Day 1, $\overline{X} = 18.1$ g, $SE = 1.5$ g; Day 2, $\overline{X} = 19.8$ g, $SE = 1.6$ g; Day 3, $\overline{X} =$

20.6 g, SE = 1.7 g). Both pygmy rabbits and cottontails consumed less total food (sagebrush + basal diet) when less basal diet was available ($F_{1,63}$ = 24.96, $P < 0.001$; Table 2), but increased total consumption as the trial progressed ($F_{1,63}$ = 5.95, P = 0.01; Day 1, $\overline{X}$ = 34.5 g, SE = 1.4 g; Day 2, $\overline{X}$ = 36.2 g, SE = 1.5 g; Day 3, $\overline{X}$ = 37.1 g, SE = 1.6 g). The proportion of sagebrush leaves versus stems consumed also differed between rabbit species ($F_{1,9}$ = 63.44, $P <$ 0.001) and with the amount of basal diet offered ($F_{1,63}$ = 27.12, P < 0.001; Fig. 4), but not with sex ($F_{1,9}$ = 2.08, P = 0.18) or day of trial ($F_{1,63}$ = 0.08, P = 0.77), and the species × sex interaction was not significant ($F_{1,9}$ = 0.27, P = 0.62). Pygmy rabbits consumed a greater proportion of leaves than did cottontails, and both species consumed a greater proportion of leaves when they were offered more basal diet (Fig. 4).

Diameters of stems cropped by free-ranging and captive rabbits.— Pygmy rabbits and cottontails cropped and consumed branches of sagebrush differently. Both captive and free-ranging pygmy rabbits at Cedar Gulch (captive $\overline{X}$ = 0.97 mm, SE = 0.01 mm; free-ranging $\overline{X}$ = 0.68 mm, SE = 0.01 mm) cropped sagebrush stems at diameters that were about one-half the size of those cropped by cottontails (captive $\overline{X}$ = 1.80 mm, SE = 0.11 mm; free-ranging $\overline{X}$ = 1.20 mm, SE = 0.07 mm; $F_{1,28}$ = 38.62, $P < 0.001$). However, free-ranging rabbits on average cropped smaller diameters than did their captive counterparts ($F_{1,28}$ = 15.12, $P < 0.001$). By cropping a smaller stem diameter, pygmy rabbits consumed a greater proportion of sagebrush leaves versus stems than did cottontails ($F_{1,28}$ =54.76, $P < 0.001$), and the species × captivity status interaction was significant ($F_{1,28}$ = 8.85, P = 0.006), but captivity status across species of rabbit was not significant ($F_{1,28}$ = 0.007, P = 0.94). We noted that all of the captive mountain cottontails cropped larger average diameter stems than did pygmy rabbits, consuming the middle part of the sagebrush branch, and discarding the leafier, apical stems with smaller diameters. In contrast, none of the captive pygmy rabbits discarded parts of the stem. These observations held true when finding and measuring stem diameters of free-ranging rabbits. Apical stems of cropped sagebrush branches discarded by cottontails were smaller in diameter than diameters cropped from shrubs ($F_{1,22}$ = 18.57, $P < 0.001$), and captive cottontails cropped and discarded larger diameter stems than free-ranging cottontails ($F_{1,22}$ = 20.77, $P < 0.001$). Diameters of the discarded apical stems of cropped branches from cottontails (captive $\overline{X}$ = 1.23 mm, SE = 0.03 mm; free-ranging $\overline{X}$ = 0.53 mm, SE = 0.01 mm) were similar in size to diameters of cropped branches from pygmy rabbits ($F_{1,28}$ = 3.57, P = 0.07), but captive rabbits cropped and discarded larger diameter stems than free-ranging rabbits ($F_{1,28}$ = 76.01, $P < 0.001$) and the interaction between stem diameter cropped or discarded × captivity status was significant ($F_{1,28}$ = 12.90, P = 0.001).

The apical parts of the branches that cottontails discarded had a similar average proportion of leaves as the sagebrush branches consumed by pygmy rabbits ($F_{1,28}$ = 0.16, P = 0.69), suggesting that these 2 species select opposing sections of sagebrush branches. Additionally, captive rabbits consumed or discarded branches with a greater proportion of leaves than did free-ranging rabbits ($F_{1,28}$ = 5.52, P = 0.03), but the proportion of leaves discarded or consumed × captivity status interaction was not significant ($F_{1,28}$ = 0.19, P = 0.67). The proportion of leaves on the branches discarded by cottontails was significantly higher than the proportion of leaves actually consumed ($F_{1,22}$ = 79.72, $P <$ 0.001) and the interaction between proportion of leaves discarded or consumed × free-ranging or captive cottontails was significant ($F_{1,22}$ = 8.85, P = 0.007), but there was no difference in the proportion of leaves consumed or discarded across captivity status ($F_{1,22}$ = 1.47, P = 0.24).

Predicted nutritional and chemical composition of diets consumed by free-ranging and captive rabbits.— Across all field sites and captive feeding trials, the proportion of sagebrush leaves consumed averaged 0.60 for pygmy rabbits and 0.24 for cottontails (Fig. 4). Using the nutritional and chemical values of sagebrush leaves and stems (Table 1), we calculated that when given a choice of leaves and stems, the diet consumed by pygmy rabbits averaged 44.7% NDF, 7.74% digestible protein (DP), and 1.6% total monoterpenes, whereas the diets of cottontails averaged 54.5% NDF, 5.2% DP, and 0.8% monoterpenes. We predicted from Fig. 2d and Table 1 that when the stem diameter of sagebrush branches containing leaves and stems increases from 1 to 5.5 mm, NDF increases according to the equation $y = 47.1X^{0.20}$, DP decreases as $y = 7.23X^{-0.35}$, and total monoterpenes decrease as $y = 1.43X^{-0.40}$.

Discussion

Our study suggests that differences in their ability to tolerate plant fiber and PSMs creates tradeoffs that drive foraging behavior by sympatric specialist and generalist leporid species in a landscape dominated by chemically defended plants. As expected, based on their relatively high tolerance for PSMs in sagebrush (Shipley et al. 2012), and relatively low tolerance to digest plant fiber (Shipley et al. 2006), free-ranging and captive pygmy rabbits consumed a diet with a greater proportion of sagebrush, and they consumed a greater proportion of sagebrush leaves relative to stems, than did cottontails. For both species, the proportion of sagebrush, proportion of leaves versus stems, and stem diameters cropped differed among field sites, the availability of other food resources, and between free-ranging and captive rabbits. However, the greater-than-expected consumption of sagebrush and larger stem diameters cropped by cottontails suggests that dietary overlap, thus competition, may be greater than we predicted and previously suggested by others (Johnson and Hansen 1979; MacCracken and Hansen 1984). Across the 3 field sites, sagebrush composed 59 – 99% of the winter diet of free-ranging pygmy rabbits, which was similar to winter diets reported for pygmy rabbits in southeastern Idaho (Green and Flinders 1980b) and central Washington (Thines et al. 2004). Although the diets of free-ranging mountain cottontails in our study contained about one-half as much sagebrush (i.e., 11 – 43%) as the sympatric pygmy rabbits, the proportion of their diet consisting of sagebrush was substantially greater than previously reported for mountain cottontails in sagebrush habitats in southeastern Idaho (i.e., < 5%; Johnson and Hansen 1979; MacCracken and Hansen 1984). Therefore, our findings suggest that at some sites in winter, sagebrush might be a more important food source for mountain cottontails than previously believed. This unexpectedly large dietary overlap between pygmy rabbits and cottontails also suggests a lower degree of resource partitioning at the plant scale and a greater potential for competition than we predicted.

Not only did pygmy rabbits consume more sagebrush, but they also consumed a several-fold greater proportion of leaves relative to stems than did cottontails. We saw the same pattern in diets of free-ranging rabbits reconstructed from plant fragments in feces and bite marks on sagebrush, and in captive rabbits when sagebrush leaves and stems were offered in separate bowls, and on intact branches with leaves. Furthermore, both in the field and in captivity, mountain cottontails reduced the proportion of sagebrush leaves they consumed by cropping stems at larger diameters than did pygmy rabbits, and by discarding the smaller-diameter apical stems that had a greater proportion of leaves. As a result, mountain cottontails minimized the monoterpenes they consumed. Discarding the apical portion of woody plants, both with and without leaves, also has been observed in other leporids, such as black-tailed jackrabbits (*Lepus californicus*) consuming sagebrush (Anderson and Shumar 1986), European rabbits (*Oryctolagus cuniculus*) consuming pine (*P. radiata*) and *Eucalyptus* (*E. nitens* and *E. globulus*) seedlings (O'Reilly and McArthur 2000), and snowshoe hares (Pease et al. 1979) and mountain hares (Pulliainen and Tunkkari 1987) consuming woody vegetation. By consuming 2.5 times greater proportion of leaves, pygmy rabbits consumed a sagebrush diet that was 18% lower in fiber, 50% higher in digestible protein, and twice as high in total monoterpenes than the sagebrush diet consumed by cottontails. In addition, sagebrush leaves had a greater relative proportion of β-pinene than did stems. β-pinene was the individual monoterpene that was most avoided by both pygmy rabbits and cottontails in captive experiments (Nobler 2016). Regardless, the perceived relative "risk" of consuming diets with higher fiber and higher monoterpenes predicted by the relative risk model (Camp et al. 2015) was similar (2.9 – 3.3) for both rabbit species, suggesting that tradeoffs made between fiber and PSMs when consuming whole sagebrush in natural habitats are relatively similar to those made by captive rabbits on artificial diets.

The differences we observed in sagebrush consumption by sympatric pygmy rabbits and mountain cottontails conformed to expectations based on their physiology and body size. In experiments with captive animals, pygmy rabbits voluntarily consumed up to 5 times more 1,8-cineole, a major monoterpene in sagebrush, and demonstrated a greater capacity to minimize systemic exposure to cineole than did cottontails by minimizing absorption and maximizing detoxification of ingested cineole (Shipley et al. 2012). On the other hand, cottontails digested fiber (e.g., plant cell wall) 40% better than did pygmy rabbits (Shipley et al. 2006). In addition, cottontails, which are 2-3 times larger, have larger mouths and teeth, and greater jaw strength, which enables them to crop stems at the larger diameters observed here, and as shown with a wide variety of herbivores (Shipley and Spalinger 1992; Wilson and Kerley 2003). Cropping larger bites increases harvesting rate (Gross et al. 1993), potentially reducing the time spent foraging (Spalinger et al. 1988; Rominger et al. 1996; Bergman et al. 2001), reducing the time herbivores are exposed to predators (Ferguson et al. 1988), and diluting toxins in the leaves (Wiggins et al. 2006). Like cottontails, mountain hares (~3.5 kg) and snowshoe hares (~1.4 kg) have been reported to crop high-fiber stems at diameters averaging 3-4 mm and still maintain their body weight on low-quality, woody vegetation during the winter despite their digestive limitations (Pease et al. 1979; Pehrson 1983).

Although we found similar patterns of sagebrush consumption in each of our experiments, we found differences in the intensity of use of sagebrush plants and leaves by free-ranging rabbits across field sites and between free-ranging and captive animals. These differences in selected diets might be attributed to differences in the composition of PSMs in sagebrush (i.e., diversity versus concentration), types and amounts of alternative foods available (i.e., senescent vegetation versus commercial rabbit pellets), environmental conditions (e.g., temperature, snow depth), animal requirements (e.g., thermoregulation, activity), and different previous experiences. For example, PSMs and nutrient content of sagebrush varies across the region (Frye et al. 2013). Ulappa et al. (2014) found that sagebrush leaves from

Magic Reservoir, where our rabbits consumed less sagebrush, had a lower concentration of crude protein, a less-diverse monoterpene profile, and higher concentration of camphor, a monoterpene that deters feeding by pygmy rabbits (Shipley et al. 2006), cottontails (Nobler 2016), and snowshoe hares (Sinclair et al. 1988) than leaves from Cedar Gulch, where rabbits consumed the most sagebrush. When plants contain a less-diverse monoterpene profile, the higher concentration of a few individual monoterpenes can overwhelm individual detoxification pathways (Dearing et al. 2000; Kohl et al. 2016). However, further studies are necessary to better understand the effects of individual monoterpenes and monoterpene diversity on sagebrush used by both species of rabbits.

The availability of alternative food resources also may explain differences in sagebrush composition in diets across sites and in captivity. For example, free-ranging pygmy rabbits in Washington consumed twice as much sagebrush during winter when high-quality grasses and forbs were less available than during summer (Thines et al. 2004). In our study, rabbits consumed more sagebrush and sagebrush leaves at Cedar Gulch, which had a lower cover of forbs and grasses on mima mounds and fewer sub-shrubs between mounds than in Rocky Canyon (Parsons et al. 2016). Furthermore, differences in snow depth could reduce the availability of dwarf species of sagebrush (e.g., low sagebrush, *A. arbuscula*) that are considered more palatable than Wyoming big sagebrush (Frye et al. 2013; Rosentreter 2005). Likewise, our experiments with captive leporids and those of Shipley et al. (2006) showed that pygmy rabbits and cottontails will increase their intake of sagebrush or sagebrush leaves when the availability of other high-quality food decreases. The fact that we controlled the quality and amount of sagebrush and alternative foods available to captive rabbits likely explains the differences in the proportion of leaves and stem diameters cropped by captive versus free-ranging rabbits. However, source locations of captive rabbits or length of time in captivity, which may compromise functional capacity of host and associated gut microbes to tolerate PSMs and fiber (e.g., Kohl and Dearing 2012; Kohl et al. 2014), might have contributed to these differences. The increase in sagebrush consumption over the 3 days of our feeding experiments with captive rabbits supports this hypothesis.

Our findings provide new insight into how specialist and generalist herbivores share food sources within sagebrush-steppe communities. Despite the higher-than-expected dietary overlap, differences in the amount and plant parts consumed by pygmy rabbits and cottontails suggests a degree of diet partitioning. For example, small but significant differences in diet or intake of energy such as those seen between the golden mouse (*Ochrotomys nuttalli*; specialist) and the white-footed mouse (*Peromyscus leucopus*; generalist) can lead to resource partitioning rather than competition (Gibbes and Barrett 2011). On the other hand, the different foraging behaviors of pygmy rabbits and cottontails may actually increase, rather than decrease, resource competition. Unless pygmy rabbits consume the clippings left by cottontails, browsing on larger sagebrush branches by cottontails would reduce the amount of smaller-diameter stems branching above the severed area that would be available to pygmy rabbits. In contrast, removal of small stem diameters by pygmy rabbits is unlikely to have an effect on cottontails that reject this portion of the stem. However, if sagebrush plants increased investment in leaves compared to stems (e.g., brooming; Christie et al. 2014) and induce PSMs in response to relatively high levels of browsing by pygmy rabbits (Ulappa et al. 2014), pygmy rabbits could indirectly alter availability of acceptable large stem diameters with low concentrations of leaves for cottontails. However, if pygmy rabbits consume sagebrush clippings left by cottontails, they might obtain high-quality food at a lower foraging cost. In that case, cottontails might facilitate, rather than compete with, pygmy rabbits. Because we do not have data to confirm or deny that pygmy rabbits consume clippings left by cottontails, we cannot conclude for certain if the differences observed in foraging strategies lead to resource partitioning, potential competition, or even facilitation. Furthermore, the extent of potential competition or facilitation between the rabbit species depends on their absolute and relative abundance within the same sagebrush landscape, and the quantity and quality of available alternative forages, which can vary greatly over time and space (Price and Rachlow 2011). For example, our observations of fresh rabbit pellets at hundreds of sagebrush plants during winter and on over 50 mima mounds during summer within our study areas indicated that 3-30% of all plants and > 80% of all mima mounds were used by either or both species, and that pygmy rabbit density exceeded that of cottontails in these sites by 1 – 2 orders of magnitude (J. Rachlow, personal observation). Furthermore, in one of the few studies that examined competition between a specialist and generalist feeder, Schleuter and Eckmann (2008) found that dietary overlap, and presumably competition, between the benthic specialist, ruffe (*Gymnocephalus cernuus*), and the perch (*Perca fluviatilis*), a dietary generalist, decreased when food resources declined, because the perch switched to alternative food resources. This suggests that cottontails may not use sagebrush habitats with low abundance of alternative forages.

The differential use of sagebrush plants by pygmy rabbits and cottontails also might play a role in ecosystem dynamics. Sagebrush shrubs are relatively slow-growing and intolerant of browsing (Bilbrough and Richards 1993), but little is known about the effects of removing leaves and stems at different diameters, or concentrating browsing only on leaves, as does the sage-grouse (Frye et al. 2013). Moderate browsing can cause some big sagebrush to grow faster (Messina et al. 2002), but intensive grazing on Wyoming big sagebrush by ungulates decreases the number of sagebrush shrubs, and the amount of concealment cover they provide (Singer and Renkin 1995). Sagebrush plants subjected to sustained, intensive browsing by pygmy rabbits around burrow systems have higher levels of crude protein content and some monoterpenes (Ulappa et al. 2014), and reduced canopy and live vegetation (Parsons et al. 2016). However, sagebrush plants around burrow systems of pygmy rabbits exhibited higher rates of seed production and seedling recruitment over time, suggesting that pygmy rabbits have a positive effect on sagebrush regeneration (Parsons et al. 2016). This implies that long-term effects of intensive foraging on the vegetative community may be positive for species inhabiting sagebrush-steppe ecosystems that rely on sagebrush for concealment from predators, even if short-term effects on the vegetative community may influence these species negatively. In addition to cropping larger stems diameters of sagebrush, cottontails discarded apical branches with leaves, which might contribute to nitrogen recycling and re-uptake into the sagebrush and perennial grasses as they decompose (Evans and Black 1993; Cardon et al. 2013). Additionally, the above-ground biomass of Wyoming big sagebrush increases significantly when the soil is treated with nitrogen (Miller et al. 1991), and several native perennial grasses also respond to increased nitrogen levels from decomposing sagebrush leaf litter (Schlatterer and Tisdale 1969). The magnitude of such potential effects and the consequences of browsing sagebrush by cottontails have not been examined, but like pygmy rabbits, cottontails might influence plant growth, reproduction, and species composition over time. Understanding how these 2 leporid species use the same food sources in different ways can advance our understanding of mechanisms of coexistence, competition, or facilitation between dietary specialists and generalists, and also suggest avenues for research into how they might contribute differently to and alter ecosystems dynamics over time.

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Supplementary Data

Supplementary Data SD1. – Full protocol for steam distillation run on leaf, 1-mm, 3-mm, and 5-mm stems from 5 distinct areas near the Cedar Gulch site in the Lemhi Valley of Idaho, USA.

Supplementary Data SD2. – Settings and sequence parameters for monoterpene quantification using a gas chromatograph and headspace auto-sampler.

Supplementary Data SD3. – Monoterpene composition of oils extracted from Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) leaves, and stems cut at 1-mm, 3-mm, and 5-mm diameters.

Supplementary Data SD4. – Description of morphology, average proportion of leaves ± standard error, average stem diameter ± standard error, and average dry matter (DM) mass of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*; leaves + stems) ± standard error for each of 6 branch morphologies offered to each captive pygmy rabbit (*Brachylagus idahoensis*) and mountain cottontail rabbit (*Sylvilagus nuttallii)* during stem diameter trials.

Figure Legends

Figure 1. Experimental set-up and example of 6 different branch morphologies of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) used during captive feeding trials to determine stem diameters cropped by pygmy rabbits (*Brachylagus idahoensis*) and mountain cottontail rabbits (*Sylvilagus nuttallii*).

Figure 2. Dry leaf mass (a), stem mass (b), total mass (c), and the proportion of leaves versus stems (d) in relation to diameter of branches of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) collected at the Cedar Gulch field site in the Lemhi Valley of Idaho, USA during January 2015.

Figure 3. Percentages (mean ± *SE*) of sagebrush (*Artemisia* spp.), other shrubs, grasses and sedges, and forbs consumed by a) pygmy rabbits (*Brachylagus idahoensis*; *n* = 10 at Cedar Gulch, 9 at Rocky Canyon, 10 at Magic Reservoir), and b) mountain cottontails (*Sylvilagus nuttallii*; *n* = 10 at Cedar Gulch, 11 at Rocky Canyon, 10 at Magic Reservoir) at 3 field sites in Idaho, USA, during January 2014. An asterisk denotes significant differences in percent sagebrush consumed between rabbit species ($\alpha = 0.05$). Letters signify differences in sagebrush consumption among field sites and across rabbit species.

Figure 4. A comparison of the proportion (mean ± *SE*) of sagebrush (*Artemisia* spp.) leaves versus stems consumed by free-ranging pygmy rabbits (*Brachylagus idahoensis*) and mountain cottontail rabbits (*Sylvilagus nuttallii*) at 3 field sites in Idaho, USA during January 2014 (first 3 bars), free-ranging (FR) and captive pygmy rabbits and mountain cottontails when cropping bites from whole sagebrush branches at or collected from Cedar Gulch during January 2015 and 2016 (fourth and fifth bars), and captive pygmy rabbits and mountain cottontail rabbits when offered separated Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) leaves and stems collected from Cedar Gulch during January 2014 with 50% and 25% of their basal diet (BD, sixth and seventh bars). Capital letters signify differences between field sites. Lower case letters signify differences between amount of basal diet, and an asterisk denotes significant differences between rabbit species ($\alpha = 0.05$).

Table 1. Dietary quality of composite Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) samples collected from Cedar Gulch study area in eastern Idaho during January 2015. Different letters within a row denote significant differences among plant parts.

Sagebrush constituent	Leaves	1-mm stems	3-mm stems	5-mm stems
Neutral detergent fiber (%)	33.90	60.94	71.92	76.12
Acid detergent fiber (%)	14.13	37.48	44.66	47.11
Acid detergent lignin (%)	8.13	18.94	20.65	20.52
Acid-insoluble ash (%)	0.71	1.43	1.91	2.40
Dry matter digestibility (%)	61.27	35.05	26.66	23.67
Crude protein (%)	15.57	7.92	6.38	6.08
Digestible protein content (g N/100 g)	10.58	3.48	2.05	1.77
Total monoterpene content (% oil extracted per g)	2.44 ± 0.41^{A}	0.31 ± 0.12^{B}	0.19 ± 0.07^{B}	0.13 ± 0.04^{B}
β-pinene (% of total monoterpene content)	28.75 ± 1.38^{A}	24.74 ± 1.31^{AB}	24.33 ± 1.98^{AB}	21.86 ± 1.43^{B}
1,8-cineole (% of total monoterpene content)	4.04 ± 0.41^{A}	1.99 ± 0.21^{B}	1.97 ± 0.24^{B}	1.53 ± 0.09^{B}
Camphor (% of total monoterpene content)	7.79 ± 1.32^{A}	6.26 ± 1.49^{A}	8.05 ± 1.46^{A}	8.31 ± 1.59^{A}

Table 2. Consumption of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) sagebrush by captive pygmy rabbits (*Brachylagus idahoensis*; *n* = 8) and mountain cottontail rabbits (*Sylvilagus nuttallii*; *n* = 5) when offered a supplementary high-protein, low-fiber pelleted basal diet at 25% and 50% of their normal basal diet consumption during February and March 2014. Different letters within rows denote significant differences between species × diet combinations.

Rabbit species	Pygmy rabbits		Mountain cottontails	
Basal diet	25%	50%	25%	50%
Proportion sagebrush consumed	0.77 ± 0.01^{A}	0.47 ± 0.01^{BC}	0.54 ± 0.04^{B}	0.34 ± 0.02^{C}
Sagebrush consumed (g DM)	24.28 ± 1.29^{A}	17.25 ± 1.05^{A}	20.09 ± 3.12^{A}	14.73 ± 1.33^{A}
Total consumed (g DM)	33.70 ± 1.30^{A}	35.70 ± 1.05^{A}	33.92 ± 3.12^{A}	42.01 ± 1.35^{A}