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Differences in dietary niche and foraging behavior of sympatric mule and white-tailed deer

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Abstract. Mule (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) are congeneric and share similar life histories, yet their distribution is segregated across much of North America. Extensive research on both species within and outside their zone of co-occurrence has not fully explained these distribution patterns, especially the potential role of diet and foraging behavior. Therefore, we used a common garden experiment to compare diet composition, diet quality, foraging behavior, and intake of tractable mule and white-tailed deer foraging together within the dry Douglas-fir (*Pseudotsuga menziesii*)/ponderosa pine (*Pinus ponderosa*) forests of northeastern Washington. We sampled at 21 0.5-ha sites from June to August 2016. We used standard bite count techniques coupled with forage biomass sampling, behavioral observations, and nutritional analyses to compare the foraging ecology of the two species. Mule and white-tailed deer had similar activity patterns. However, mule deer took larger bites and harvested food faster than white-tailed deer, and white-tailed deer consumed more diverse but higher-quality diets than mule deer. These differences resulted in mule deer acquiring ~25% more dry matter and digestible energy per day. About 90% of the diets consumed by both deer species consisted of deciduous shrubs and forbs, and they selected many of the same plant species. However, overall diet composition was 38% dissimilar, with mule deer consuming diets that were more likely to contain shrubs with higher levels of tannins and lower levels of dry matter digestibility than diets eaten by white-tailed deer. Dietary overlap was greatest at both very low and very high forage biomass, indicating potential for modest resource competition or partitioning. Our research provides evidence that differences in diet composition of mule and white-tailed deer do not merely reflect differences in habitat selection, but also suggest the species differ in their fundamental nutritional niches.

Key words: competition; deer; diet composition; diet quality; dietary overlap; Douglas-fir; foraging behavior; intake rate; niche; nutrition; *Odocoileus;* ponderosa pine.

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INTRODUCTION

North America is home to the only two deer species of the *Odocoileus* genus, mule (*O. hemionus*) and white-tailed deer (*O. virginianus*). Both species share similar morphology and life history characteristics, and can hybridize in sympatric areas (Derr 1991, Bradley et al. 2003). These deer species are medium-sized (adult females range from 40 to 90 kg in North America), browsing

ruminants that are considered habitat and dietary generalists, but their distributions are segregated across much of their ranges (Anderson and Wallmo 1984, Smith 1991). Mule deer and subspecies (*O. h. sitkensis* and *O. h. columbianus*) are distributed across the west and north, whereas white-tailed deer (*O. virginianus*) are primarily distributed across the eastern and southern parts of North America. Nevertheless, their distributions currently overlap across a broad north–south zone primarily along the Rocky Mountains from Canada to Mexico (Hygnstrom et al. 2008, NatureServe, http://explorer.natureserve.org/servlet/NatureServe, Fig. 1). Despite extensive research on mule and white-tailed deer where they are allopatric and sympatric (Fig. 1, Table 1), the mechanisms responsible for this distribution pattern remain unclear, and in particular, the role nutritional requirements and foraging behavior have received little attention.

Studies comparing the realized niches of mule and white-tailed deer have produced varied conclusions about the degree of resource partitioning between these species. Studies of sympatric populations suggest that overlap in space use, habitat use and selection, and diet composition varies from very little to extensive, depending on location and season. For example, although their home range sizes are similar, habitat overlap between the two species varies from <5% (Wood et al. 1989, Whitney et al. 2011) to >40% (Whittaker and Lindzey 2004, Brunjes et al. 2009) and tends to be highest in summer (Walter et al. 2011). Although in some areas mule and white-tailed deer use the same habitats (Anthony and Smith 1977, Lingle 2003), several studies have suggested that mule and white-tailed deer partition habitat based on their different adaptations for avoiding predators and thermoregulating. For example, white-tailed deer run faster and signal conspecifics with tail-flagging, whereas mule deer have a unique stotting gait and larger ears (Geist 1981, Mackie et al. 1998, Lingle 2002, 2003, Haskell et al. 2010). In addition, the mule deer's lower critical temperature, which is lower than that of white-tailed deer, suggests a greater cold tolerance (Mautz et al. 1985). Therefore, in many areas mule deer select steeper, more rugged

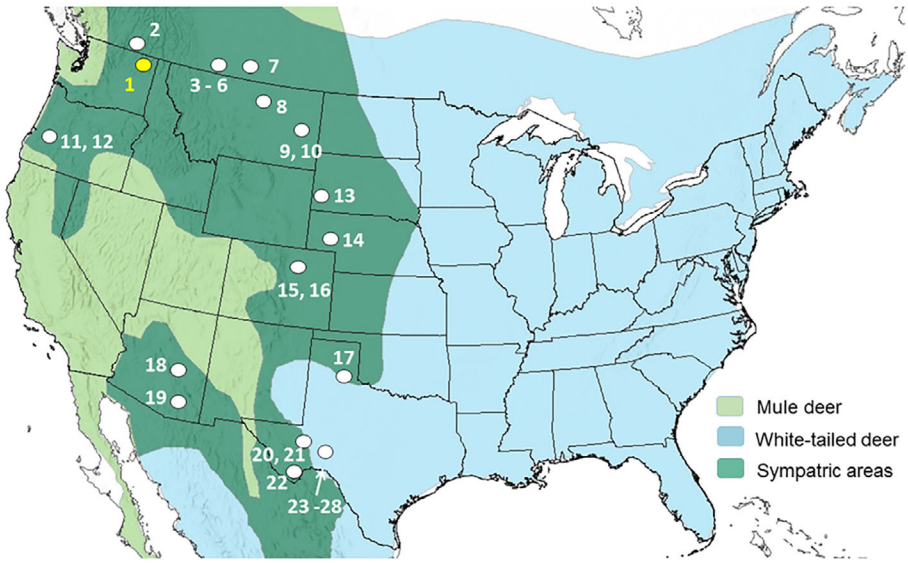

Fig. 1. Distributions of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) across North America, which overlap across a north–south zone primarily along the Rocky Mountains, including eastern Washington in the northwestern United States (NatureServe, http://explorer.natureserve.org/servlet/NatureServe). The yellow dot (1) indicates the location of this study, white dots indicate the locations of previous studies comparing ecology of mule and white-tailed deer within the zone of sympatry, and numbers indicate the reference and information about the studies found in Table 1.

Table 1. Region, general habitat, elevation, and general topics investigated in 31 studies of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) where their distributions overlap in North America.

Map key	Citation	Region	Topic
1	This study	Colville National Forest, NE Washington	Nutrition, food habits, foraging behavior
2	Robinson et al. (2002)	Siwash/Kootenay Mtn., S British Columbia	Maternity, recruitment, survival, predation
3	Lingle (2001)	S Alberta	Anti-predator strategies, group patterns
4	Lingle (2002)	S Alberta	Predation, habitat segregation
5	Lingle (2003)	S Alberta	Group formation
6	Lingle and Wilson (2001)	S Alberta	Predator detection and avoidance
7	Kramer (1973)	Cypress Hills, S Alberta	Interspecific behavior, dispersion
8	Martinka (1968)	Bear Paw Mtn., N Montana	Range use, food habits
9	Wood et al. (1989)	Prairie Co., E Montana	Ecology, spatial distribution
10	Mackie et al. (1998)	Montana	Review of ecology and management
11	Smith (1987)	Umpqua River Basin, SW Oregon	Dispersion, habitat use
12	Whitney et al. (2011)	N Umpqua River, W Oregon	Resource partitioning
13	Zimmerman et al. (2006)	Black Hills, W South Dakota	Digestive morphology
14	Walter et al. (2011)	North Platte River Valley, W Nebraska	Resource selection, movement, home range
15	Whittaker and Lindzey (2001)	Rocky Mountain Arsenal, NE Colorado	Population characteristics
16	Whittaker and Lindzey (2004)	Rocky Mountain Arsenal, NE Colorado	Spatial distribution, habitat use
17	Bradley et al. (2003)	Kent County, NW Texas	Hybridization
18	McCulloch (1973)	Tonto National Forest, S Arizona	Diet and nutrition
19	Anthony and Smith (1977)	San Cayetano/Dos Cabezas Mtn., SW Arizona	Habitat and nutritional ecology
20	Wiggers and Beasom (1986)	Trans-Pecos/Panhandle, Texas/SE New Mexico	Habitat
21	Stubblefield et al. (1986)	Trans-Pecos Region, W Texas	Hybridization
22	Krausman (1978)	Chisos Mtn., Texas	Nutrition, forage use
23	Avey et al. (2003)	Crockett Co., W Texas	Spatial ecology
24	Brunjes et al. (2006)	Crockett Co., W Texas	Habitat use
25	Brunjes et al. (2009)	Crockett Co., W Texas	Home range size and overlap
26	Butler et al. (2009)	Crockett Co., W Texas	Parturition, fawn bedding sites
27	Haskell et al. (2010)	Crockett Co., W Texas	Postpartum behavior, grouping patterns
28	Haskell et al. (2008)	Edwards Plateau, W Texas	Parturition
29	Derr (1991)	Southwest United States	Hybridization
30	Hygnstrom et al. (2008)	West and Midwest United States	Review of species movements
31	Ballard et al. (2001)	Western North America	Review of deer–predator relationships

Note: Spatial locations of the studies are depicted in Fig. 1 using the map key, except 29–31, which were regional studies.

topography at higher elevations, whereas white-tailed deer select areas with more concealment cover (e.g., riparian areas, denser shrub, and canopy cover) and edge habitats (Wiggers and Beasom 1986, Mackie et al. 1998, Avey et al. 2003, VerCauteren 2003, Butler et al. 2009, Walter et al. 2011, Whitney et al. 2011).

Although the two species exhibit some partitioning of cover and topography, the degree to which nutritional resources are partitioned between mule and white-tailed deer is less clear. Several studies have suggested that the two species use similar vegetation associations where their distributions overlap (Anthony and Smith 1977, Whittaker and Lindzey 2004, Brunjes et al. 2009, Walter et al. 2011), but dispute the relative importance of habitat that provides high-quality forage. Some have suggested that white-tailed deer favor landscapes with agricultural crops and can survive and reproduce more successfully

when consuming the high-quality forage those crops provide (Kramer 1973). Others (Stewart et al. 2000) suggested that mule deer tend to select habitats with higher-quality forage than white-tailed deer. Sympatric populations of mule and white-tailed deer generally eat similar diets, but the degree of dietary overlap ranges from less than 50% to over 90% depending on location and season (Martinka 1968, Anthony and Smith 1977, Krausman 1978, Mackie et al. 1998, Whittaker and Lindzey 2004, Brunjes et al. 2009, Whitney et al. 2011). Diet overlap between species is expected to be greatest in marginal habitats when nutritious food is scarce (Brunjes et al. 2009). For example, diet composition of sympatric mule and white-tailed deer in Colorado overlapped by about 40% in summer but increased to 70% in winter when plants were scarce and of low quality (Whittaker and Lindzey 2004). Studies of digestive anatomy are likewise ambiguous (Clauss et al. 2009 vs. Zimmerman et al. 2006), although Robbins et al. (1987*a*) did not detect differences in digestive efficiency between the deer species when consuming an early-season grass.

To date, no study has answered the question of what drives variation in dietary overlap between deer species across their ranges. One hypothesis is that they differ in their ability to harvest, digest, and detoxify forages (i.e., their fundamental dietary niche). If so, then diet overlap will depend on the type and amount of forage available in their shared habitat and would be expected to increase as the amount of nutritious forage in their shared habitat declines. An alternative hypothesis is that disparate diets are simply a consequence of the deer species using different habitats that correspond with their distinctive adaptations for evading predation and withstanding temperature extremes. In that case, the extent of dietary overlap would depend on the degree of similarity in forage resources between those different habitats. Previous studies have been unable to distinguish these competing hypotheses because diet composition was confounded with habitat use. Diets reconstructed from plant fragments in feces and ruminal digesta collected from free-ranging deer reflect foods consumed and digested over several days as animals move across habitats and microhabitats that can vary considerably in available plant species (Martinka 1968, Anthony and Smith 1977, Krausman 1978, Mackie et al. 1998, Whittaker and Lindzey 2004). Furthermore, these studies were unable to simultaneously compare foraging behavior, nutritional quality of diets, and nutrient intake between the deer species. This knowledge gap is important because these nutritional metrics are related to population performance and directly affect pregnancy, twinning rates, and fawn survival (Robinette et al. 1973, Tollefson et al. 2010, 2011).

To address this question, we compared nutritional ecology of mule and white-tailed deer in a common garden experiment in which tractable individuals of each species were allowed to forage together in the same habitats across a wide range of forage conditions in Douglas-fir (*Pseudotsuga menziesii*)/ponderosa pine (*Pinus ponderosa*) forests in northeastern Washington. Optimal foraging theory predicts that herbivores seek to maximize their rate of nutrient intake (e.g., digestible energy and protein) subject to the constraints imposed by the plant resources available (Hanley 1997, Shipley et al. 1999). Therefore, we predicted that if the fundamental dietary niches of mule and white-tailed deer are truly distinct in terms of tolerance for plant fiber and secondary metabolites, nutrient requirements, and mechanics of harvesting, we would detect differences in their diet composition and foraging behavior when they foraged in the same space at the same time. We also predicted that when forage biomass was low, diets of sympatric deer would overlap more as they attempted to subsist with limited resources. Testing these hypotheses will help clarify how differences in dietary niches might reduce competition and drive habitat segregation, or how habitat segregation might prevent dietary competition between herbivore species with very similar dietary niches. Furthermore, because both mule deer and white-tailed deer have high ecological, cultural, recreational, and economic value (Ballard et al. 1999), understanding the behavioral and physiological factors that influence their respective distributions and areas of co-occurrence might help wildlife and land managers to better understand their responses to habitat changes and the mechanisms that drive population performance.

Materials and Methods

Study area

We conducted our study on the Colville National Forest located in northeastern Washington, United States (48.6599° N, 117.6230° W), an area of current and historic overlap between mule and white-tailed deer (Fig. 1). Colville National Forest encompasses 4451 km^2 including portions of the Okanagan, Kettle River, and Selkirk mountains within the western foothills of the Rocky Mountains (U.S. Forest Service [USFS] 2017). Topography varied from flat, open fields to high-elevation peaks and basins. Elevation ranged from 650 to 1400 m. Temperatures were cold with frequent snowfall in winter, followed by hot and dry summers. Annual temperatures ranged from 2.6°C in winter to 31.3°C in summer, and annual precipitation was 53 cm (U.S. Climate Data 2017).

Plant communities varied in our study area, ranging from xeric Douglas-fir/ponderosa pine plant associations to mesic western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) associations. Major understory plants included huckleberry (*Vaccinium membranaceum*), ninebark (*Physocarpos malvaceus*), snowberry (*Symphoricarpos albus*), bearberry (*Arctostaphylos uva-ursi*), and pinegrass (*Calamagrostis rubescens*). In addition to mule and white-tailed deer, our study area supported populations of elk (*Cervus canadensis*), moose (*Alces alces*), and domestic cattle, and predators such as cougars (*Puma concolor*), black bears (*Ursus americanus*), wolves (*Canis lupus*), and coyotes (*Canis latrans*).

Experimental animals

Because our goal was to compare foraging behavior and activity between mule and white-tailed deer without the confounding effects of habitat or maternal learning, we used a common garden experimental design. We raised female neonates of both deer species together under identical conditions to ensure consistent nutritional and learning experiences. Fawns were obtained from licensed wildlife rehabilitators across eastern Washington, including Asotin, Pend Oreille, Spokane, and Yakima counties (Washington State Scientific Collection Permit 14-206) when they were <72-h old in June–July 2014 and 2015. Age at acquisition was estimated based on information from rehabilitators, condition of umbilical cords, hoof development, size, and response to fear or sudden movement. Animals were housed at Washington State University's (WSU) Wild Ungulate Facility when not participating in field experiments. All husbandry and experimental procedures for the animals were approved by WSU's Institutional Animal Care and Use Committee (IACUC protocols #4454, #4161).

Female fawns of both species were group-housed and bottle-fed deer milk replacer (Fox Valley DayOne 30/40; Animal Nutrition, Lake Zurich, Illinois, USA) following feeding schedules similar to Parker and Wong (1987) to mimic natural feeding and growth patterns of maternally raised fawns. Fawns were also offered a nutritionally balanced grain-alfalfa pelleted deer diet (Tollefson et al. 2010), pasture grass, alfalfa (*Medicago sativa*), and soil (for developing rumen microbes) as their rumens developed and after weaning at 150 d. We supplemented the maintenance diets with local shrubs and forbs such as willow (*Salix* spp.), serviceberry (*Amelanchier alnifolia*), oceanspray (*Holodiscus discolor*), clover (*Trifolium* spp.), and fireweed (*Chamerion angustifolium*) to acquaint fawns with the different types of vegetation they would encounter during field experiments. Fawns were habituated to human observers and to loading and traveling in a stock trailer. We weighed fawns every 3–4 d during their first 2 months of life, once per month after weaning, and before and after each field season.

Selection and preparation of field sites

To compare foraging behavior and activity of mule and white-tailed deer across a variety of forest conditions where the species naturally overlapped within our study area, we selected 21 sites within the dry Douglas-fir/ponderosa pine plant association. Sites covered a range of past harvest types and ages-since-harvest, from 1 to 20 and un-harvested areas. Our sites were located within areas of observed spring and summer ranges of local deer. Sites ranged from 709 to 1372 m elevation and varied in aspect. However, sites were restricted to areas with <20% slope and that were accessible by passable roads so we could build fencing and transport tractable deer to the sites. We determined the order in which the field sites were sampled based on plant

phenology (e.g., starting with lower elevation sites), and we alternated sampling between the east and west sides of the Kettle Crest. We used data provided by the Colville National Forest to identify sites that met our criteria. Within each site, we constructed one 0.5-ha temporary deer pen using a 2 m tall plastic mesh barrier with three strands of electric fencing on the inside. The size of the pen was selected to ensure all deer had access to the range of understory plants found within each site for the 1–3 d during which they were confined to the pen.

Stand characteristics and forage biomass

Before placing deer in the temporary pen at each site, we measured forest stand characteristics and understory vegetation biomass. We established four evenly spaced line transects perpendicular to the longest baseline of each pen. Canopy closure was estimated from 20 equally spaced locations along each transect using a point-intercept densitometer; canopy closure at each site was calculated as the mean proportion of obstructed intercepts among transects. Available understory vegetation was measured in 8, 2-m^2 circular microplots that were evenly spaced along transects. We clipped all vegetation within the microplots from 0.5 cm to 1.5 m from the ground (the range a deer can reach while foraging), identified, and sorted each plant by species and plant part (leaves and stems for woody shrubs, new and old growth for evergreens and conifers). Plants were placed in labeled paper bags, transported to WSU, dried at 100°C for 24 h to a constant weight, and then weighed to the nearest 0.01 g. Understory biomass (kg/ha) for each site was estimated as the mean of the eight microplots within each site. Within each site, we also calculated percent availability of each plant functional group and species, plant species richness, and species diversity (Shannon's *H*).

Foraging behavior and food intake of deer

In June 2016 when the female deer were 1–2 yr old, four mule deer and four white-tailed deer were transported to the study area. We exchanged one mule deer mid-season because of difficulties loading her into the trailer; thus, five total mule deer were used in the experiments. Two weeks before being transported to the field sites, we fed deer plants native to eastern Washington to help transition them from pelleted feed to natural forages. After they arrived at the study area, deer were no longer fed pellets and were housed in an acclimation pen within a forest stand with sufficient natural forage available for 5 d before data collection began. All animals were placed in the same pen at the same time and generally remained in the enclosure for 60 h. Insufficient vegetation to support eight deer for 60 h required us to remove animals from four stands after 24 h. In each site, deer were allowed a 4-h acclimation period before we began collecting behavioral and foraging data. We weighed each deer before and after the field season to the nearest 2 kg.

To compare the mechanics of foraging, diet composition, and nutrient intake between mule and white-tailed deer, we conducted six foraging trials per deer in each site during daylight hours. Bite count methods were similar to those used by Wagoner et al. (2013), Ulappa (2015), and Denryter et al. (2017). Trials occurred when deer were naturally and actively foraging without prompting from observers. To be considered a foraging trial, deer had to actively feed for 15 min (i.e., no lapses in foraging >3 min; if a 3-min lapse occurred, the trial was ended and resumed when the deer began foraging again). During each foraging trial, one of two trained observers followed an individual deer close enough to record on a digital audio recorder the number of bites, plant species of each bite taken, and a visual estimate of each bite size. If an observer was not able to identity a plant to species or genus when species identification was not possible, then it was identified to functional group. Unknown plant bites identified to functional group made up <0.01% of all observed bites. During foraging trials, observers also estimated distance the deer traveled (m) while foraging by counting their own steps as they walked with the animal and calculating the total distance from their average pace length. Observers alternated between deer of different species and individuals to ensure data were collected similarly for both species.

To estimate mean bite size (g/bite) for each combination of plant species, deer species, and site, we collected 10 representative bites that matched the observed size and plant part. Representative bites were placed in a labeled paper bag, dried at 100°C for 24 h, and weighed to the nearest 0.01 g. Mean bite rate (bites/min) per

animal per site was calculated as the total number of bites cropped per site divided by the total length of all foraging trials at that site. Vegetation mass consumed while foraging (g) was the sum of the product of bite size and number of bites taken of each plant species. Mean bite size (g/bite) was the forage mass divided by the number of bites, and harvest rate (g/min) was the product of mean bite rate and mean bite size.

To compare time spent foraging per day between mule and white-tailed deer, we collected continuous activity data across the 24-h day from each animal using an accelerometer (MotionWatch 8; CamNtech, Boerne, Texas, USA) attached to a radio-collar. Accelerometers were programmed to record a value based on triaxial motion each minute across the 3-month field season. Values ranged from 0 (no motion detected) to 3000 (high motion detected). We calibrated the accelerometer data from 36 h of focal behavioral observations of each deer in ~2-h time blocks between 07:00 and 21:00 h over the 3-month study period. Behaviors we recorded on an electronic tablet included bedded, bedded and ruminating, standing, foraging, walking, and running. To create a complete activity record for the time spent in each site, we used the behavioral observations to calibrate the 1-min accelerometer data using methods similar to those of Naylor and Kie (2004) and Wagoner et al. (2013). Calibration accuracy averaged 84.4% (standard deviation [SD] = 3.4%) for all behaviors and 89.1% (SD = 2.9%) for foraging. We used the calibration values to calculate the minutes foraged per day per animal per site. The actiwatch malfunctioned for one white-tailed deer while at four sites, so for those we used the average foraging time for that deer across other sites adjusted by the difference between the mean and the observed foraging time for that pen for the other white-tailed deer. These four sites for this animal were not used for comparing foraging time between deer species but were used in calculations of daily intake. Daily dry matter intake (DMI, g/d) was the product of harvest rate and time spent foraging per day.

Diet composition and selection

We determined the composition by mass of plant functional groups (deciduous shrubs, forbs, evergreen shrubs, graminoids, conifers, ferns, and other) and plant species in deer diets and in the available biomass for each site and deer. We calculated plant species richness and plant species diversity using Shannon's diversity index (*H*) for each animal's diet within each site using the vegan package (Oksanen et al. 2017) in R (R Core Team 2017) version 3.4.2. We calculated a selection index for each plant functional group and individual plant species based on its proportion in the diet and in the plot for each animal and site using Ivlev's Electivity Index (Ivlev and Scott 1961). To calculate an overall index value for each plant, at least two individuals of each deer species had to have eaten the plant within a site, and at least six sites had to have an index value before averaging values across all sites for each deer species. We calculated the standard error (SE) and 95% confidence interval (CI) for each electivity index value. Individual plants and functional groups were classified as either selected (mean index value was positive and the CI did not include 0), neutral (CI overlapped 0), or avoided (mean index value was negative and CI did not include 0).

Nutritional content of forages and nutrient intake by deer

To determine the dry matter digestibility (DMD, %), digestible energy (DE, kJ/g), and digestible protein (DP, g protein/100 g forage) content of deer diets, observers collected simulated diets for each deer at the conclusion of each day's foraging trials by collecting the plant species and parts that were consumed during foraging trials in the observed proportions and bite sizes. These simulated diets were stored on ice and transferred to a freezer within 1–2 d. All diets were then transported to WSU for nutritional analysis. To determine the nutritional quality of plants consumed by mule and white-tailed deer, we also collected fresh samples of plant species and parts that were prevalent in the habitat at each site and in deer diets. Multiple composite samples for each plant species were collected throughout the field season and across the study area. Plant samples were buried in ice for several days in the field until being transferred to a freezer and stored until analysis.

Before laboratory analyses, samples were freeze-dried and ground to pass a 1-mm screen. Using sequential detergent analysis including

sodium sulfite and alpha amylase, we determined the neutral detergent fiber, acid detergent fiber, acid detergent lignin, and acid insoluble ash of each sample (Goering and Van Soest 1970, Mould and Robbins 1981, Ankom Fiber Analyzer 200/220; Ankom Technology, Fairport, New York, USA). We also determined the gross energy content of each simulated diet and forage species using a bomb calorimeter (C5000; IKA Works, Wilmington, North Carolina, USA) and nitrogen content (%) using a Carbon-Nitrogen TruSpec analyzer (LECO, St. Joseph, Michigan, USA). We estimated crude protein content (%) as 6.25 × the nitrogen content (Robbins 1993). Finally, we determined the biological activity of tannins in the diets and major plant species by measuring tannin-specific protein-binding capacity (mg bovine serum albumin precipitate/mg forage, hereafter "tannin content") using the precipitation assay of Martin and Martin (1982). We estimated DMD and DP from summative equations developed and tested in mule, black-tailed, and white-tailed deer (Robbins et al. 1987*a*, *b*, Hanley et al. 1992, Parker et al. 1999). We calculated DE for all samples from gross energy content × DMD. We estimated daily digestible energy intake (DEI, MJ/d) as the product of DMI and DE and daily digestible protein intake (DPI, g protein/d) as the product of DMI and DP.

Statistical analyses

We compared body mass of deer averaged across the field season and the body mass lost during the field season using a two-sample *t* test for equal variances. We then compared bite size, bite rate, harvest rate, foraging time, diet quality, and daily nutrient intake rates between deer species across field sites using linear mixed-effects models with restricted maximum-likelihood estimation (Zuur et al. 2009). Proportion of time spent active, standing, foraging and walking, time spent foraging, bite size, bite rate, harvest rate, travel rate, DMD, DE, DP, tannin content, DMI, DEI, DPI, species richness, and diversity of diets were used as response variables in 23 individual models. Dry matter intake, DEI, and DPI were analyzed on daily and per d/kg basis. The fixed effect in all models was deer species, and individual deer crossed with site was the grouping variable for specifying a random intercept. Examination of residuals vs. fitted values showed no violation of the assumption of homogeneity of variance across all models. We fit models using the lme4 package (Bates et al. 2015) in R (R Core Team 2017) version 3.4.2. Model coefficients were considered statistically significant when their associated 95% CI did not overlap zero.

To compare diet composition between deer species across sites, we used a Bray–Curtis nonmetric multidimensional scaling (NMDS) ordination analysis (Bray and Curtis 1957, Beals 1984). We compared diet dissimilarity in terms of both proportion of individual plant species and plant functional groups in the diets of each deer. We compared diet composition within and across all 21 sites and used deer species as our grouping factor. When comparing diet dissimilarity within sites, we included only the individual deer that foraged at that site (usually 8). When comparing diet dissimilarity across sites, we averaged diet composition for each deer across all sites in which that deer foraged (usually 21, although one of the five mule deer foraged in the first nine sites and another for the remaining 12 sites, with only four of each species together at one time). Ordinations were considered acceptable at stress values ≤ 0.1. We then applied a permutational multivariate analysis of variance (perMANOVA) to each set of ordinations based on the central value of each deer species to compare overall dissimilarity (Anderson 2001). We used contrasts to identify which plants or functional groups had the most influence on differences in diet composition and compared those plants and functional groups using two-sample *t* tests. All ordination comparisons were conducted using the vegan package (Oksanen et al. 2017) in R. We examined the relationship between diet dissimilarity and available and non-conifer understory plant biomass by fitting linear regression models, and we evaluated curvilinear fits (i.e., log-linear and polynomial models) after examining residuals.

Finally, we conducted a post hoc analysis to determine which physical and nutritional characteristics of plants might explain diet dissimilarity between mule deer and white-tailed deer. We first used MANOVA to determine whether characteristics of the 22 plants with the most influence on diet dissimilarity differed between the species overall and nine additional plants that contributed to dissimilarity in the five sites with

the highest dissimilarity. We then used one-way ANOVA to examine which specific characteristics differed significantly between the deer species. For this model, the response variables included functional group (i.e., shrub vs. other), proportion of the plant in the total available biomass across all sites, average bite size for both deer species, DMD, DE content, DP content, and tannin content, and the independent variable was deer species.

Results

The 21 sites included in our study varied in both physical and vegetation characteristics (Table 2). In particular, we observed 10-fold differences across sites in the amount of vegetation biomass available to deer. While together within these 21 sites, mule and white-tailed deer demonstrated similar activity patterns during the day. Both deer species spent half of their day active (i.e., not bedded) and about 44% of their day (~650 min, 10.5 h) foraging. Deer spent a very small proportion of their day standing and walking/running independent of foraging, and those proportions did not differ between deer species (Table 3).

Mean body mass did not differ significantly between mule ($\bar{X}$ = 54.0 kg, SE = 4.0) and white-tailed deer ($\bar{X}$ = 49.1 kg, SE = 4.6) during the three-month field season (t = 0.81, P = 0.46), and both species lost a similar amount of mass during that period (mule deer: $\bar{X}$ = 3.8 kg, SE = 1.3 kg, white-tailed deer: $\bar{X}$ = 0.4 kg, SE = 1.9 kg, t = 1.58, P = 0.16). Despite their similar body mass, mule deer ate food faster than white-tailed deer but consumed a lower-quality diet (Table 3). Mule deer took larger bites but cropped them at a similar rate as white-tailed deer, which resulted in higher overall harvest rates. Although both deer species foraged for the same amount of time per day and traveled at the same rate while foraging, mule deer had a ~25% higher DMI because of their higher harvest rate (Table 3). However, their DMI per kg body mass was similar (Table 3). Conversely, the diets of white-tailed deer were higher in DP and lower in tannin content than those consumed by mule deer, although they did not differ in DMD, CP, and DE. Regardless of their slightly lower-quality diet, the higher daily DMI by mule deer allowed them to achieve a higher overall DEI, but DEI/kg body mass, DPI, and DPI/kg body mass were similar between the species (Table 3).

Table 2. Overall site characteristics of the 21 sampled sites within the Colville National Forest in northeastern Washington from June to August 2016.

Site characteristics	Mean	SD	Min	Max
Elevation (m)	1120	203	708	1372
Slope (°)	14.8	6.3	3	28.8
Overstory canopy cover (%)	58.0	18.7	26.3	95.0
Overstory canopy height (m)	21.9	6.6	9.3	35.1
Basal area (m^2)	5.1	2.4	1.9	10.7
Available biomass (kg/ha)	889.7	510.8	146.7	1927.1
Non-conifer biomass (kg/ha)	757.1	441.9	84.2	1706.3
Deciduous shrubs (kg/ha)	322.0	291.3	3.6	1339.9
Forbs (kg/ha)	152.3	121.3	8.8	425.7
Evergreen shrubs (kg/ha)	508.3	512.4	17.2	1848.3
Graminoids (kg/ha)	212.0	209.3	13.4	577.3
Conifers (kg/ha)	212.2	290.0	0.0	990.6

Diet composition of mule and white-tailed deer was similar with respect to plant functional groups. Overall diet dissimilarity, as measured by NMDS, was only 16.2% (stress = 0.02, F = 2.71, P = 0.07, Fig. 2a). About half of the diets of both deer species consisted of deciduous shrubs, and more than a quarter of the diets were forbs (Table 4). Evergreen shrubs, graminoids, conifers, ferns, and plants classified as other (lichens and mushrooms) were also eaten by deer, but each accounted for <10% of their overall diets (Table 4). On the other hand, evergreen and deciduous shrubs each composed about a quarter of the available biomass, and forbs, graminoids, and conifers each composed about 15% (Table 4). Consequently, deciduous shrubs as a whole were classified as selected (i.e., significantly positive selection index) by mule deer and neutral (i.e., confidence overlapped 0) by white-tailed deer, whereas forbs were classified as neutral for mule deer and selected for white-tailed deer (Table 4). Both deer species avoided conifers, evergreen shrubs, and graminoids (i.e., all had significant negative selection indices, Table 4). Ferns, lichens, and mushrooms were too rare in the sites to develop an accurate selection index, but deer were observed digging for mushrooms and pulling lichens off trees.

Although mule and white-tailed deer both consumed diets consisting mainly of deciduous

Table 3. A comparison of foraging behavior and diet quality between five female mule deer (*Odocoileus hemionus*) and four female white-tailed deer (*Odocoileus virginianus*) foraging in the same 21 forest stands within Colville National Forest in northeastern Washington from June to August 2016 (mean with standard error in parentheses).

Foraging variables	Mule deer	White-tailed deer	β estimate†
Proportion time active	0.497 (0.018)	0.504 (0.025)	0.007 (−0.042, 0.056)
Proportion time bedded	0.503 (0.018)	0.496 (0.025)	−0.007 (−0.056, 0.042)
Proportion time foraging	0.445 (0.015)	0.452 (0.020)	0.007 (−0.032, 0.047)
Proportion time standing	0.033 (0.007)	0.029 (0.01, 0.05)	−0.004 (−0.023, 0.015)
Proportion time walking	0.020 (0.005)	0.023 (0.007)	0.003 (−0.010, 0.016)
Foraging time (min/d)	641 (21)	652 (29)	11 (−46, 68)
Travel rate (m/min)	3.0 (0.4)	4.0 (0.5)	1.0 (−0.1, 2.1)
Bite size (g/bite)	0.128 (0.007)	0.110 (0.007)	−0.018 (−0.032, −0.003)*
Bite rate (bite/min)	17.2 (1.1)	15.6 (1.4)	−1.62 (−4.41, 1.18)
Harvest rate (g/min)	2.21 (0.17)	1.70 (0.19)	−0.50 (−0.89, −0.11)**
Dry matter intake (g/d)	1387.9 (103.5)	1110.1 (109.7)	−277.8 (−515.6, −35.7)*
Dry matter intake ($g \cdot d^{-1} \cdot kg^{-1}$ body mass)	26.07 (2.69)	23.20 (3.55)	−2.88 (−9.88, 4.14)
Diet dry matter digestibility (%)	62.4 (0.6)	63.8 (0.8)	1.5 (−0.1, 3.0)
Diet crude protein (%)	10.79 (0.28)	11.13 (0.20)	0.34 (−0.08, 0.75)
Diet digestible energy (kJ/g)	11.58 (0.10)	11.76 (0.09)	0.18 (−0.01, 0.37)
Diet digestible protein (g/100 g)	5.52 (0.24)	5.98 (0.18)	0.45 (0.07, 0.83)*
Diet tannin content (mg BSA precipitate/mg forage)	0.053 (0.005)	0.041 (0.004)	−0.012 (−0.020, −0.004)*
Digestible energy intake (MJ/d)	16.10 (1.28)	13.02 (1.52)	−3.08 (−6.10, −17.47)*
Digestible energy intake ($MJ \cdot d^{-1} \cdot kg^{-1}$ body mass)	0.30 (0.03)	0.27 (0.04)	0.03 (−0.11, 0.05)
Digestible protein intake (g protein/d)	78.65 (7.84)	66.70 (8.25)	−11.95 (−28.46, 4.88)
Digestible protein intake (g $protein \cdot d^{-1} \cdot kg^{-1}$ body mass)	1.48 (0.18)	1.39 (0.22)	0.10 (−0.54, 0.35)
Diet richness (no. of plants)	25.2 (2.1)	30.4 (2.5)	6.2 (1.2, 11.12)*
Diet diversity (Shannon's *H*)	2.04 (0.09)	2.25 (0.10)	0.21 (0.01, 0.41)*

Notes: BSA, bovine serum albumin. Beta estimates (with 95% confidence interval [CI] in parentheses) are from linear mixed-effects models where deer species was included as a categorical predictor variable and mule deer were used as the reference category.

† Coefficients for difference between deer species and 95% CIs were determined by crossed effects mixed models, and significance (indicated by the asterisk) was determined by non-overlapping CIs.

shrubs and forbs, we observed significant clustering of the composition of individual plant species within deer diets (stress = 0.05, $F = 1.55$, $P = 0.03$). Across all diets, dissimilarity was 37.7% (Fig. 2b), and ranged from 43.6% to 70.2% among sites. Diet dissimilarity across field sites was primarily driven by 22 plants ranging from <0.1% to 11.4% of the diet, with nine additional plants influencing dissimilarity at individual sites (Table 4). Polynomial models best described the relationship between diet dissimilarity and available plant biomass ($F_{2,18} = 5.44$, $P = 0.01$) and non-conifer biomass ($F_{2,18} = 8.22$, $P = 0.003$, Fig. 3). We expected that diets of the two deer species would differ most when available plant biomass was the greatest but found that their diets differed most when forage resources were either high or low. Overall, characteristics of the 31 plants that had the most influence on within-site dissimilarity (Table 4) differed between mule deer and white-tailed deer (Wilks' lambda = 0.50, $F = 4.21$, $P = 0.005$). Shrubs were consumed more heavily by mule deer ($F = 14.89$, $P = 0.0006$) and had a lower DMD ($F = 7.30$, $P = 0.01$) and higher tannin content ($F = 5.71$, $P = 0.02$). Plant species consumed differently by the two deer species did not differ in available biomass ($F = 2.39$, $P = 0.13$), average bite size ($F = 0.03$, $P = 0.87$), or DP content ($F = 0.78$, $P = 0.39$).

Despite overall differences in diet composition, eight plant species were ranked in the top 10, proportionally, in average diets across all sites for both deer species (Table 5). Also, from the 60 individual plant species that met our minimum criteria for calculating a selection index, mule deer selected 11 plant species, avoided 21, and showed no selection for 28 (Table 5). White-tailed deer selected 13 plant species, avoided 18,

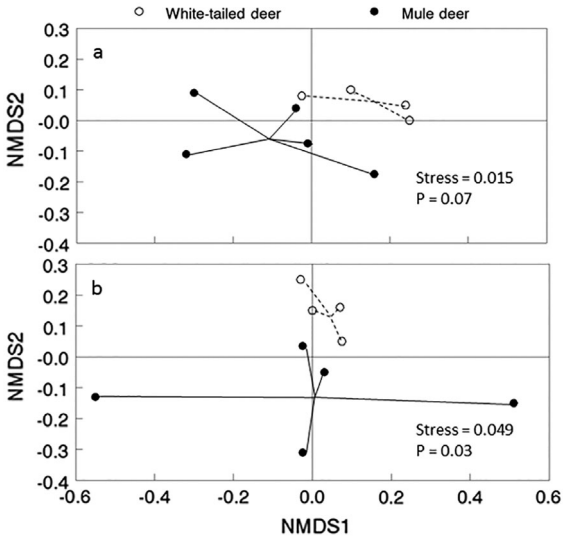

Fig. 2. Diet dissimilarity between five female mule deer (*Odocoileus hemionus*) and four female white-tailed deer (*Odocoileus virginianus*) as measured by non-metric multidimensional scaling (NMDS) of (a) seven plant functional groups (dissimilarity = 16.2%), and (b) 116 plant species (dissimilarity = 37.7%) while foraging in the same 21 forest stands in Colville National Forest in northeastern Washington between June and August 2016. Diets were calculated as mean proportion of each functional group and species for each deer across all 21 sites.

and showed no selection for 29 (Table 5). Within functional groups, 86% of all deciduous shrubs and 77–84% of all forbs were categorized as selected or neutral by both deer species, whereas all but one conifer, one evergreen shrub, and one graminoid were avoided (Table 5).

Diets of the two deer species also differed in plant species richness and diversity. Across all 21 sites combined, mule deer consumed an average of 92 (SE = 17) different plants, whereas white-tailed deer consumed 107 plants (SE = 5). Within sites, diets of white-tailed deer averaged 25% richer in species (i.e., five more plant species) and had a higher diversity index than did those of mule deer (Table 3).

Discussion

By comparing foraging behavior and nutritional ecology of mule and white-tailed deer that were raised together under identical conditions, we were able to identify key differences between the deer species that are independent of maternal care or differential habitat selection. Although the foraging behavior of mule and white-tailed deer was generally similar, we detected modest differences in their realized dietary niches and foraging behavior that may contribute to niche partitioning when residing in sympatric populations. Within dry Douglas-fir/ponderosa pine habitats in northeastern Washington where they naturally co-occur, both species spent the same amount of time foraging, but used somewhat different foraging strategies. Mule deer cropped larger bites and harvested food faster than white-tailed deer, whereas white-tailed switched among plant species more frequently to consume more nutritious and diverse diets. As a result, mule deer acquired more dry mass and DE per day overall, but not relative to body mass, than did white-tailed deer. Although diets of mule and white-tailed deer contained similar proportions of plant functional groups, especially deciduous shrubs and forbs, plant species in deer diets were 37.7% dissimilar across field sites and were most dissimilar when total available and non-conifer biomass was either very low or high.

One of the most notable differences between the nutritional ecology of the deer species while feeding together at the same sites was that mule deer achieved a ~25% greater DMI and DEI than did white-tailed deer overall, but a similar DMI and DEI relative to body mass, which ranged over 20 kg among individuals within each species. Digestible energy intake is especially important to female deer in summer and early fall when they must meet competing demands for lactation and acquiring enough body reserves for the fall breeding season and for winter survival. For example, Tollefson et al. (2010, 2011) found that DEI of lactating mule deer in October influenced pregnancy, twinning rates, milk quality, fawn growth, and fawn survival. On average, DEI and DPI of our non-lactating young mule deer just met estimated summer maintenance requirements for adult females (15.7 MJ/d, 80 g protein/d, Parker et al. 1999, Tollefson et al. 2010, Hanley et al. 2012, Wagoner et al. 2013). In contrast, our white-tailed deer fell slightly below estimated adult maintenance values of DEI and

Table 4. Characteristics (mean with standard error in parentheses) of individual plant species that contributed the most to dissimilarity of the diets of five female mule deer (*Odocoileus hemionus*) and four female white-tailed deer (*Odocoileus virginianus*) foraging in the same 21 forest stands in Colville National Forest in northeastern Washington in June–August 2016.

Functional group and plant species	Plant biomass (%)	Mule deer diet (%)	White-tailed deer diet (%)	Bite size (g)	Tannin content	DMD (%)	DE (kJ/g)	DP (g/100 g forage)
Deciduous shrub	25.2 (4.2)	58.2 (5.0)	45.6 (2.7)		0.071	66.9	12.6	6.6
Acer glabrum	0.7 (0.5)	4.5 (1.6)[10]	2.6 (0.3)	0.12	0.134	66.2	11.9	5.4
Alnus viridis	0.5 (0.4)	2.5 (0.5)	0.9 (0.3)	0.19	0.131	62.4	12.2	8.4
Amelanchier alnifolia	1.9 (0.6)	11.4 (2.1)[1]	9.5 (1.0)[1]	0.11	0.079	60.9	11.3	6.1
Corylus cornuta	0.4 (0.3)	1.1 (0.3)	1.0 (0.6)	0.11	0.169	50.0	8.8	4.4
Holodiscus discolor	0.3 (0.2)	2.3 (1.0)	0.7 (0.1)	0.06	0.019	69.4	13.1	7.2
Lonicera utahensis	0.9 (0.5)	6.1 (2.4)[4]	4.6 (0.3)[9]	0.09	0.000	69.7	12.8	6.1
Ribeslacustre†	<0.1	0.7 (0.3)	0.8 (0.2)	0.09	0.099	66.4	12.1	6.1
Rosa spp.	1.5 (0.3)	7.1 (0.7)[3]	6.4 (0.6)[3]	0.11	0.174	64.9	11.5	4.3
Rubus parviflorus	0.4 (0.2)	1.2 (1.0)	1.0 (0.3)	0.29	0.177	67.3	11.5	5.1
Salix spp.	0.3 (0.2)	8.4 (1.5)[2]	5.3 (0.6)[5]	0.16	0.138	60.6	12.2	6.5
Shepherdia canadensis	2.0 (1.2)	2.0 (0.8)	2.4 (0.9)	0.12	0.060	67.9	12.7	10.3
Symphoricarpos albus	4.6 (1.8)	5.1 (2.7)[6]	4.8 (0.7)[7]	0.08	0.000	68.0	13.0	7.0
Forb	13.1 (2.5)	28.7 (4.3)	41.8 (3.8)		0.026	59.9	10.5	5.0
Arnica cordifolia	1.3 (0.6)	4.7 (1.1)[9]	7.4 (0.9)[2]	0.10	0.000	68.6	10.7	2.8
Clintonia uniflora	0.1 (<0.1)	0.5 (0.3)	1.9 (0.5)	0.07	0.000	67.5	11.5	5.0
Cornus canadensis	1.0 (0.5)	2.5 (1.1)	5.7 (1.4)[4]	0.13	0.147	62.7	11.0	4.2
Epilobium watsonii†	0.1 (<0.1)	0.6 (0.4)	0.3 (0.1)	0.05	0.000	45.2	8.0	5.3
Eurybia conspicua†	0.1 (<0.1)	0.6 (0.3)	1.4 (0.3)	0.28	0.000	68.8	12.1	5.6
Fragaria virginiana	1.0 (0.3)	4.8 (1.2)[7]	4.7 (1.1)[8]	0.08	0.143	65.7	11.3	3.6
Goodyera oblongifolia†	0.1 (<0.1)	<0.1	0.7 (0.2)	0.05	0.000	68.3	13.9	6.2
Heuchera cylindrica†	0.2 (0.2)	0.7 (0.2)	0.3 (0.1)	0.06	0.169	61.8	10.9	3.4
Hieracium spp.†	0.5 (0.2)	0.3 (0.1)	0.8 (0.2)	0.05	0.000	62.1	11.2	3.9
Lupinus sericeus	1.5 (0.8)	5.4 (0.8)[5]	4.5 (0.8)[10]	0.15	0.000	57.4	10.5	12.8
Maianthemum stellatum	0.4 (0.2)	0.3 (0.2)	1.3 (0.3)	0.12	0.000	63.3	10.9	6.9
Sedum spp.†	0.2 (0.2)	0.5 (0.3)	0.1 (<0.1)	0.06	0.048	60.2	10.6	1.0
Taraxacum officinale	0.2 (0.1)	0.7 (0.2)	1.8 (0.2)	0.06	0.000	69.5	11.8	6.5
Viola spp.†	0.3 (0.1)	0.5 (0.3)	0.9 (0.1)	0.04	0.000	56.2	8.9	7.8
Evergreen shrub	29.9 (4.8)	7.8 (1.8)	3.7 (0.5)		0.078	57.3	11.2	4.2
Arctostaphylos uva-ursi	15.2 (4.3)	4.8 (1.7)[8]	1.3 (0.2)	0.17	0.136	52.2	10.8	2.2
Linnaea borealis	9.5 (2.7)	1.9 (0.7)	1.3 (0.3)	0.06	0.000	50.9	9.3	3.7
Graminoid	16.0 (2.7)	1.1 (0.4)	1.1 (0.2)					
Poa spp.†	0.2 (0.2)	0.1 (0.1)	0.2 (0.1)	0.08	0.000	54.2	9.3	4.1
Lichen (*Bryoria* spp.)	<0.1	2.8 (0.9)	5.1 (1.6)[6]	0.15	0.000	72.5	12.8	1.7
Mushroom (*unknown*)	<0.1	<0.1	1.7 (0.5)	0.28	0.000	82.0	14.5	21.2
Conifer	13.3 (3.5)	1.0 (0.3)	0.2 (0.1)		0.078	46.6	10.1	1.7
Fern	<0.1	<0.1	<0.1					

Notes: For deciduous and evergreen shrubs, nutritional values including tannin content (mg bovine serum albumin precipitate/mg forage), dietary dry matter digestibility (DMD), dietary digestible energy (DE), and dietary digestible protein (DP) are for current annual growth leaves only, but the other categories contain all current growth. Numbers in superscript in the diet columns are ranks.

† Plant species contributed to dissimilarity only in sites where diets were most dissimilar.

DPI. Regardless, DEI in our study fell within the ranges reported for captive and free-ranging deer by others (Alldredge et al. 1974, Holter et al. 1977, Sadleir 1982, Galbraith et al. 1998, Kuzyk and Hudson 2006, Wagoner et al. 2013, Ulappa 2015).

Although mule deer are often perceived to be larger than white-tailed deer, mean body mass of

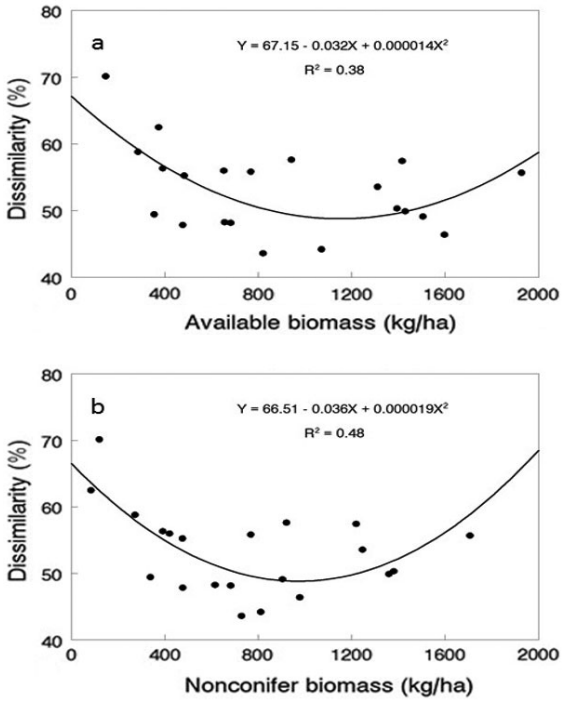

Fig. 3. The relationship between dissimilarity (computed using non-metric multidimensional scaling) of plant species consumed by five female mule deer (*Odocoileus hemionus*) and four female white-tailed deer (*Odocoileus virginianus*) and (a) total available understory plant biomass, and (b) non-conifer understory plant biomass. Deer were observed foraging in the same 21 forest stands in Colville National Forest in northeastern Washington between June and August 2016.

the yearling and two-year-old deer in our study did not differ between species across the summer field experiment. Body mass of live, sympatric wild mule and white-tailed deer has not been reported, though many studies have handled both deer species for research (e.g., deploying radio collars and collecting tissue samples). However, one study reported the mass of female mule deer carcasses was 5–8 kg heavier on average than carcasses of white-tailed deer where they shared summer range in the Black Hills of South Dakota (Zimmerman et al. 2006). Adult body size depends on region, genetics, and animal experiences such as maternal care and forage quality. For example, body size of mule deer varies among subspecies (Anderson and Wallmo 1984) and body size of white-tailed deer increases with latitude (Smith 1991). In addition, diet quality and nutritional status of female mule deer influence their milk quality and thus growth of their fawns (Tollefson et al. 2010, 2011). Therefore, differences in body size of wild mule and white-tailed deer may result in part from their location and their use of different habitats and food plants. Parsing the effects of phylogeny on body size from the effects of diet and habitat selection will require more information about body mass of mule and white-tailed deer across the zone of overlap.

Our findings suggest that white-tailed deer in our study had a lower DEI than mule deer because they traded off larger bites and higher harvest rates for smaller bites and higher-quality diets. On average, white-tailed deer took bites 15% smaller than those of mule deer, thus harvested forage 25% more slowly, but their diets were higher in DP and lower in tannin content than those of mule deer foraging in the same stands (although DE was similar). Smaller bites are often more nutritious because they exclude the more fibrous stems and older leaves of plants (Wilson and Kerley 2003). Similarly, the plant species consumed by white-tailed deer that contributed most to the difference in diet between the species were higher in DMD, lower in tannins, and less likely to be deciduous or evergreen shrubs.

White-tailed deer might have consumed a higher-quality diet because they have a lower physiological tolerance for plant fiber, tannins, or other plant secondary compounds than mule deer. If so, this suggests that the two deer species might have different fundamental dietary niches. Although direct comparisons of digestive efficiency have yet to be conducted, Zimmerman et al. (2006) suggested that mule deer may be better able to digest a fibrous diet than white-tailed deer due to differences in digestive morphology. Both mule (Austin et al. 1989, Hagerman and Robbins 1993) and white-tailed deer (Mole et al. 1990, Shimada 2006) have relatively large parotid salivary glands and tannin-specific binding proteins in their saliva that reduce the effects of plant tannins on protein digestibility (Robbins et al. 1987*a*, *b*). Although the relative ability of the two deer species to bind plant tannins has not been directly compared, mule deer

Table 5. Plant species selection (S = selected, N = neutral, A = avoided) calculated using Ivlev's Electivity Index (IE) for five female mule deer (*Odocoileus hemionus*) and four female white-tailed deer (*Odocoileus virginianus*) foraging in the same 21 forest stands in Colville National Forest in northeastern Washington in June–August 2016.

Functional group and plant species	Mule deer			White-tailed deer		
	IE	95% CI	Selection	IE	95% CI	Selection
Deciduous shrub	0.35 (0.34)	0.01, 0.43	S	0.30 (0.31)	−0.01, 0.37	N
Acer glabrum	0.92 (0.34)	0.72, 1.11	S	0.90 (0.22)	0.76, 1.04	S
Alnus viridis	0.79 (0.31)	0.48, 1.10	S	0.37 (0.76)	−0.49, 1.24	N
Amelanchier alnifolia	0.70 (0.44)	0.48, 0.92	S	0.81 (0.20)	0.71, 0.90	S
Holodiscus discolor	0.43 (0.86)	−0.16, 1.03	N	0.39 (0.90)	−0.27, 1.06	N
Lonicera utahensis	0.78 (0.39)	0.53, 1.02	S	0.82 (0.25)	0.68, 0.96	S
Physocarpos malvaceus	−0.50 (0.66)	−0.87, −0.13	A	−0.57 (0.65)	−0.95, −0.19	A
Ribes lacustre	0.75 (0.59)	0.31, 1.19	S	0.80 (0.46)	0.45, 1.13	S
Rosa spp.	0.70 (0.35)	0.53, 0.87	S	0.71 (0.30)	0.56, 0.85	S
Rubus parviflorus	0.16 (0.85)	−0.40, 0.72	N	0.22 (0.89)	−0.36, 0.79	N
Salix spp.	0.59 (0.77)	0.18, 0.99	S	0.42 (0.87)	−0.04, 0.88	N
Shepherdia canadensis	0.09 (0.91)	−0.42, 0.61	N	0.32 (0.44)	−0.12, 0.76	N
Spiraea betulifolia	−0.02 (0.75)	−0.42, 0.39	N	0.25 (0.69	−0.09, 0.60	N
Symphoricarpos albus	−0.03 (0.74)	−0.39, 0.33	N	0.19 (0.62)	−0.11, 0.50	N
Vaccinium membranaceum	−0.52 (0.67)	−0.90, −0.14	A	−0.50 (0.63)	−0.86, −0.14	A
Forb	0.22 (0.46)	−0.25, 0.33	N	0.47 (0.35)	0.11, 0.55	S
Achillea millifolium	−0.89 (0.38)	−1.14, −0.65	A	−0.72 (0.59)	−1.10, −0.33	A
Actaea rubra	0.17 (0.89)	−1.07, 1.40	N	−0.67 (0.37)	−1.38, 0.07	N
Adenocaulon bicolor	0.15 (0.88)	−0.93, 0.61	N	0.18 (0.90)	0.62, 0.97	N
Antennaria pulcherrima	0.2 (1.01)	−0.60, 1.00	N	0.2 (1.01)	−0.60, 1.00	N
Antennaria racemosa	0.16 (0.92)	−0.39, 0.70	N	0.34 (0.86)	−0.17, 0.85	N
Arnica cordifolia	−0.06 (0.76)	−0.45, 0.34	N	0.25 (0.66)	−0.09, 0.59	N
Astragalus spp.	0.09 (1.00)	−0.66, 0.83	N	0.60 (0.73)	0.09, 1.11	S
Castilleja miniata	0.11 (1.05)	−0.92, 1.14	N	0.70 (0.60)	0.28, 1.16	S
Chamerion angustifolium	−0.07 (0.92)	−0.55, 0.41	N	0.50 (0.74)	0.13, 0.88	S
Cirsium spp.	−0.97 (0.10)	−1.06, −0.87	A	−0.58 (0.76)	−1.14, −0.02	A
Clematis occidentalis	0.64 (0.84)	−0.21, 0.96	N	0.64 (0.58)	0.18, 1.10	S
Clintonia uniflora	−0.18 (0.84)	−0.73, 0.36	N	0.39 (0.79)	0.12, 0.91	N
Collinsia parviflora	0.82 (0.54)	−1.23, −0.42	A	−0.74 (0.64)	−1.16, −0.33	A
Epilobium watsonii	−0.01 (0.91)	−0.74, 0.72	N	0.03 (0.58)	−0.55, 0.62	N
Eurybia conspicua	0.63 (0.69)	0.18, 1.08	S	0.86 (0.32)	0.66, 1.06	S
Fragaria vesca	−0.31 (0.67)	−0.63, 0.03	N	−0.47 (0.63)	−0.78, −0.16	A
Fragaria virginiana	0.10 (0.72)	−0.25, 0.46	N	0.22 (0.70)	−0.12, 0.57	N
Galium triflorum	−0.66 (0.64)	1.14, −0.18	A	−0.58 (0.57)	−1.13, 0.01	N
Goodyera oblongifolia	−0.82 (0.53)	−1.28, −0.35	A	0.23 (0.91)	−0.40, 0.86	N
Heuchera cylindrica	0.58 (0.53)	0.15, 1.01	S	0.18 (0.92)	−0.56, 0.92	N
Hieracium spp.	−0.43 (0.56)	−0.72, −0.15	A	0.02 (0.61)	−0.28, 0.32	N
Hypericum perforatum	0.28 (0.97)	−0.44, 0.99	N	0.08 (0.96)	−0.69, 0.85	N
Lilaceae spp.	0.16 (0.85)	−0.26, 0.57	N	0.64 (0.58)	0.36, 0.93	S
Lupinus spp.	0.42 (0.68)	0.06, 0.78	S	0.46 (0.65)	0.12, 0.81	S
Osmorhiza chilensis	−0.37 (0.85)	−0.85, 0.11	N	−0.12 (0.80)	−0.59, 0.35	N
Penstemon conferus	−0.40 (0.86)	−1.08, 0.29	N	−0.48 (0.81)	−1.13, 0.16	N
Potentilla spp.	0.45 (0.89)	−0.21, 1.11	N	0.28 (0.89)	−0.50, 1.06	N
Pyrola spp.	−1.00 (0)		A	−0.91 (0.34)	−1.14, −0.67	A
Taraxacum officinale	−0.08 (0.49)	−0.57, 0.41	N	0.30 (0.84)	0.14, 0.73	N
Trifolium spp.	−0.36 (0.83)	−0.83, 0.11	N	0.04 (0.83)	−0.50, 0.41	N
Viola spp.	−0.33 (0.81)	−0.75, 0.10	N	0.20 (0.78)	−0.19, 0.60	N
Evergreen shrub	−0.77 (0.32)	−1.08, 0.68	A	−0.82 (0.15)	−0.97, −0.78	A
Arctostaphylos uva-ursi	−0.78 (0.41)	−0.99, 0.57	A	−0.85 (0.22)	−0.97, −0.74	A

(Table 5. Continued.)

Functional group and plant species	Mule deer			White-tailed deer		
	IE	95% CI	Selection	IE	95% CI	Selection
Ceanothus sanguineus	0.79 (0.59)	0.21, 1.37	S	0.85 (0.49)	0.45, 1.24	S
Chimaphila umbellata	0.84 (0.23)	−1.07, −0.62	A	0.91 (0.21)	−1.04, −0.77	A
Linnaea borealis	−0.54 (0.67)	−0.91, −0.16	A	−0.46 (0.64)	−0.81, −0.11	A
Mahonia aquifolium	−0.79 (0.51)	1.09, −0.48	A	0.37 (0.75)	−0.80, 0.05	N
Pachistima myrsinites	−0.60 (0.64)	−0.97, −0.22	A	0.72 (0.58)	−1.06, −0.37	A
Graminoid	−0.93 (0.13)	−1.06, −0.89	A	−0.89 (0.15)	−1.04, −0.89	A
Agrostis spp.	−1.00 (.)		A	−1.00		A
Bromus spp.	−0.88 (0.32)	−1.06, −0.70	A	−0.88 (0.40)	−1.10, −0.66	A
Carex spp.	−0.97 (0.14)	−1.04, −0.90	A	−0.84 (0.41)	−1.05, −0.63	A
Calamagrostis rubescens	−0.99 (0.04)	−1.01, −0.97	A	−0.98 (0.05)	−1.01, −0.96	A
Elymus glaucus	0.13 (0.91)	−0.34, 0.60	N	0.07 (0.92)	−0.43, 0.57	N
Festuca spp.	−0.81 (0.51)	−1.10, −0.52	A	−0.81 (0.50)	−1.09, −0.53	A
Conifer	−0.84 (0.44)	−1.29, −0.63	A	−0.81 (0.52)	−1.33, −0.57	A
Abies grandis	−0.78 (0.67)	−1.53, −0.02	A	−1 (.)		A
Pseudotsuga menziesii	−0.86 (0.43)	−1.10, −0.63	A	−0.80 (0.51)	−1.07, −0.53	A
Thuja plicata	−0.22 (0.41)	−0.63, 0.19	N	0.08 (0.76)	−0.33, 0.50	N

Notes: CI, confidence interval; SD, standard deviation. Values in parentheses are SDs.

are the only animal species known to continuously produce proline-rich binding proteins without being induced by consuming tanniferous forages (Shimada 2006). Relative tolerance for monoterpenes found in many evergreen shrubs and conifers is also unknown, but several studies have observed mule deer consuming more of these plants than did sympatric white-tailed deer (Martinka 1968, Anthony and Smith 1977, Whitney et al. 2011). However, white-tailed deer are also known to consume winter diets consisting mostly of conifers, such as balsam fir (*Abies balsamea*), that contain high levels of monoterpenes and other plant secondary metabolites (Casabon and Pothier 2007). Even though we found no significant difference in overall composition of plant functional groups between mule and white-tailed deer diets in our study, mule deer tended to consume more evergreen shrubs and conifers than did white-tailed deer. Nevertheless, the nutritional quality of diets consumed by both species in our study was within the upper range reported for DMD, DE, and DP (Parker et al. 1999, Wagoner et al. 2013, Ulappa 2015). In fact, average diets of both mule and white-tailed deer in our study met dietary DE requirements for lactation (11.5 kJ/g, Parker et al. 1999, Tollefson et al. 2010, Hanley et al. 2012, Wagoner et al. 2013), even though none were lactating. However, white-tailed deer just met maintenance requirements for DP (5.7 g protein/100 g food) and mule deer fell slightly below maintenance requirements.

The fact that white-tailed deer consumed a more diverse diet than mule deer also supports the idea that white-tailed deer might seek or require a higher-quality diet. Overall, the diets of white-tailed deer in our study contained about 25% more plant species than those of mule deer. Similarly, diets reconstructed from plant fragments in feces were about 20% more diverse for free-ranging white-tailed deer than sympatric mule deer in Arizona (Anthony and Smith 1977), and black-tailed deer (*O. h. columbianus*) had less diverse diets than Columbian white-tailed deer (*O. v. leucurus*) in western Oregon (Whitney et al. 2011). White-tailed deer also had greater dietary richness than other sympatric large herbivores such as moose in Maine (Ludewig and Bowyer 1985), and elk and domestic cattle in northern Idaho (Kingery et al. 1996). White-tailed might have consumed a more diverse diet because they have the broadest distribution of any large ungulate in North America (VerCauteren 2003), thus encounter and consume a greater diversity of forage species. Even when sympatric, white-tailed deer have been reported to use a wider range of habitats and vegetation associations than mule (or black-tailed) deer (Whitney et al. 2011). The use of more diverse habitats by

white-tailed deer might explain differences in diet diversity between free-ranging animals, but not between deer restricted to the same habitat types, as in our study.

An alternative reason for the white-tailed deer's more diverse diet is that they might benefit nutritionally from consuming a greater variety of plant types. Dietary mixing allows generalist herbivores to better track nutritional quality of plants over space and time to acquire a more balanced suite of nutrients and, in particular, to avoid overtaxing any detoxification pathway caused by eating too much of a certain type of plant secondary metabolite (Westoby 1978, Dearing et al. 2000). However, the advantages of dietary mixing may come at the cost of reducing the rate at which food is harvested. Dietary mixing inevitably requires more time searching and harvesting smaller bites or plant parts, as we observed for white-tailed deer in our study. Thus, the greater diet diversity of white-tailed deer likely indicates a broader realized niche in terms of plant taxa, whereas their higher diet quality may simultaneously reflect a narrower fundamental niche than that of mule deer in terms of nutritional requirements and tolerances for plant secondary metabolites (Shipley et al. 2009).

Although they ate higher-quality diets, white-tailed deer did not spend more time foraging each day to compensate for slower harvest rates and to achieve similar DEI as mule deer. Both mule and white-tailed deer spent an average 10.5 h of their active time foraging, which was within the range reported in other studies of summer foraging by tractable and free-ranging mule and black-tailed deer (Wagoner et al. 2013, Ulappa 2015), and free-ranging mule deer (Alldredge et al. 1974, Collins and Urness 1983, Kie et al. 1991, Kuzyk and Hudson 2006) and white-tailed deer (LaGory et al. 1981, Sorenson and Tayler 1995, Coulombe et al. 2008, Massé and Côté 2013). White-tailed deer may not have foraged longer to increase their DEI because they were close to their estimated maintenance requirements already or because they were limited by food passage rate and rumination time.

Despite modest differences in intake and diet quality, both mule and white-tailed deer in our study consumed diets that consisted of >85% forbs and deciduous shrubs, in approximately equal amounts, during the summer, and both plant groups were classified as either selected or neutral for both deer species. The remainder of the diets consisted of evergreen shrubs, conifers, and graminoids, which were classified as avoided, and ferns, mushrooms, and lichens, which were consumed but very rarely available. Thus, diets of the two deer species were over 83% similar in composition of plant functional groups and were relatively similar to deer diets other sympatric populations (Martinka 1968, Anthony and Smith 1977, Krausman 1978, Mackie et al. 1998, Whittaker and Lindzey 2004, Whitney et al. 2011).

Although mule and white-tailed deer consumed plants from the same functional groups, the plant species composition of their diets was significantly different. When foraging in the same forest stands, which varied 13-fold in available forage biomass, diet similarity ranged from 30% to 56%, which is on the lower end of the range reported for sympatric deer in Arizona (55–67%, Anthony and Smith 1977), Colorado (40–70%, Whittaker and Lindzey 2004), and Oregon (Horn's similarity index = 0.89, Whitney et al. 2011). The lower diet similarity in our study is surprising because both deer species were confined to the same 0.5-ha enclosures for 24–60 h at each site and thus were forced to select diets from the same limited area and available forage. Because we used pre-ingestion methods to measure diet composition rather than the post-ingestion or post-digestion methods used in these other studies, we believe the dissimilarity between mule and white-tailed deer diets in our study provides a more accurate measure of true dietary partitioning by the two deer species. We measured diet composition accurately and in real time by directly observing what each animal consumed within the same habitat at the scale of the bite, uninfluenced by differential habitat use by the two species. On the other hand, diet composition determined from plant fragments in feces typically underestimates the presence of highly digestible plants such as forbs, which might make those diets seem more similar, and reflects foods eaten across a variety of habitats over a period of several days (Leslie et al. 1983). Because mule and white-tailed deer often use different habitats where their ranges overlap (Smith 1987, Wood et al. 1989, Whittaker and Lindzey

2004, Whitney et al. 2011), we would expect diets reconstructed from ruminal contents or fecal pellets of wild deer to be less, rather than more, similar relative to those we measured.

We hypothesized that diets of mule and white-tailed deer would be the most similar at sites where food was scarce, based on the premise that lower food availability would cause the two deer species to use, and potentially compete for, the same forage resources. This pattern was observed by Martinka (1968) and Whittaker and Lindzey (2004), both of whom reported greater overlap in deer diets in winter when nutritious food was scarce than in summer. In contrast, deer in our study partitioned their diets to the greatest degree when foraging together in sites with low forage biomass. Therefore, diet overlap measured in winter, when plant quality is more uniformly low, may differ from dietary overlap measured in the summer within closed-canopy forest stands that offer low plant biomass but plants that range in nutritional quality. In addition, we might have found less dietary overlap overall, and especially in sites with scarce forage, because our sites spanned a much greater range of available plant biomass than other studies of sympatric deer, from three times lower on the low end to over two times greater on the high end. For example, available forage biomass where deer were sympatric in Texas ranged from 507 to 820 kg/ha (Wiggers and Beasom 1986), whereas in our study biomass ranged from a low of 146 kg/ha to almost 2000 kg/ha.

The divergent diets of mule and white-tailed deer when food resources were in very short supply might reflect mutual niche partitioning between the deer species related to moderate levels of character displacement (i.e., differences in their fundamental dietary niche) that reduces the potential effects of exploitative competition. For example, deciduous and evergreen shrubs that offered larger bites but higher tannins and other plant chemicals were most responsible for differences in diets between mule deer and white-tailed deer when they foraged in the same sites. Similarly, Krausman (1978) found that mule deer consumed more shrubs when sympatric with white-tailed deer than when allopatric, and white-tailed deer ate more forbs where the species' populations overlapped. Alternatively, a greater divergence of diets when forage was scarce might be a result of competitive exclusion that could eventually limit productivity of one of the deer species. During our experiments, we observed extremely low levels of direct aggression among individual deer (<0.01% of all behaviors), and those were restricted to pawing (Berry 2017). The incidents of aggression that did occur did not differ between the deer species and were equally directed at members of the same and different species. Although we can rule out interference competition, the lower DMD and higher tannin content of mule deer's diets than those of white-tailed deer might indicate that white-tailed deer are a superior competitor when exploiting limited forage. However, mule deer were able to more than compensate, acquiring a higher DEI by eating faster, suggesting that differences in the dietary fundamental niche might play a role in dietary partitioning both when food was scarce and when especially abundant (i.e., significant polynomial relationship between diet dissimilarity and forage biomass). Differences in their fundamental dietary niches might also be more evident at the upper end of forage abundance because deer have more options and can consume the best foods for their unique nutritional adaptations.

In conclusion, because the North American deer species prefer and consume many of the same forages throughout the zone of co-occurrence, they have the potential to compete when forage resources are scarce, and to partition food resources based on different fundamental nutritional niches when forage is abundant. Our findings might help explain observations made by wildlife managers in some regions that white-tailed deer populations have increased or expanded their distribution in many areas along this zone of co-occurrence, potentially at the expense of mule deer populations that have concurrently declined (Martinka 1968, Ballard et al. 2001, Lemkuhl et al. 2001, Avey et al. 2003, Brunjes et al. 2006), although Anthony and Smith (1977) reported a potential mule deer expansion in traditional white-tailed deer range. Our study detected differences in the realized dietary niche (i.e., aspects of diet composition and foraging behavior) when mule and white-tailed deer foraged in the same place at the same time, which highlights the importance of conducting future studies that explicitly compare their (1)

fundamental nutritional niches (e.g., fiber digestion and tolerance to toxins) and (2) population productivity (e.g., ability to turn DE into offspring) under identical conditions in captivity and across a range of habitat conditions.

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