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Conifer Diet Choices Made by Mule Deer (*Odocoileus hemionus*) of North Central British Columbia During a Cafeteria-Style Feeding Trial

Abstract

The winter diets of northern mule deer are comprised predominantly of shrubs and trees. Included in winter diets are various species of conifers, some of which are important forestry and ornamental crop trees. Diet choices and feeding habits of mule deer utilizing conifer crops, however, have not been widely reported. Here, we document diet choices made by human-habituated mule deer from north central British Columbia during an exploratory cafeteria-style feeding trial using boughs of thirteen species of native North American and introduced European conifers. Mule deer consumed more biomass from exotic conifers (specifically pine) than from rarely encountered native conifers, and consumed the least biomass from those native conifers commonly encountered by deer in northern BC, a finding which appears to lend support to the Biotic Resistance Hypothesis. From most to least biomass consumed, deer selected Mugho pine, Scots pine, western hemlock, subalpine fir, Douglas fir, Norway spruce, Ponderosa pine, western white pine, lodgepole pine, common juniper, red cedar, black spruce, and hybrid white spruce. Analysis of Variance testing suggested that deer preferred to eat exotic Mugho and Scots pine and avoided eating commonly encountered, native black and hybrid white spruce. A relationship also existed between the biomass consumed and the number of bites taken by deer from each species, which generally indicated that deer took more bites from exotic and rarely encountered conifers, but not always. Our results suggest that northern mule deer, therefore, may be more likely to damage introduced pine and other exotics relative to native species planted in either ornamental or forest plantation settings when deer densities are high and/or browse resources are limited.

Keywords: Biotic resistance hypothesis, browse preference, cafeteria trial, conifer consumption, exotic tree, forestry

Introduction

In North America, hardwood shrubs and trees comprise the majority of the winter diet of mule deer (*Odocoileus hemionus*, Martinka 1968, Kufeld et al. 1973, Boeker et al. 1972, Dusek 1975, Kramer et al. 2015) and other browsing ungulates, especially as winter snow pack increases leaving grasses, herbs and forbs less accessible (Carpenter et al. 1979). In addition to hardwoods, coniferous species can and do make up a significant portion of mule deer seasonal diets (Anthony and Smith 1974). Depending on the population in question and where feeding opportunities exist, deer may feed predominantly

on conifers in winter (Jenkins and Wright 1987, Schmitz 1990), which is the case in several mule deer ranges in British Columbia (Willms et al. 1976, Dawson et al. 1990, Waterhouse et al. 1994, Hodder et al. 2013).

In certain regions of North America, deer will commonly feed on true fir (*Abies* spp.), Douglas fir (*Pseudotsuga menziesii*), white pine (*Pinus strobus*) and other conifers such as hemlock (*Tsuga* spp.) and can damage forest and Christmas tree plantations (Kosco and Bartolome 1983, Gill 1992, Beringer et al. 1994, Swihart and Picone 1998, Saunders and Puettmann 1999, Rooney 2001, Vourc'h et al. 2002, Vila et al. 2003). Urban deer are also known to significantly impact ornamental conifer plantings in urban and peri-urban areas, particularly in winter (Conover and Kania 1988).

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Browsing by mule deer on crops in the northwest lowers forest productivity as defined by foresters and in some cases contributes to plantation failure, leading to significant losses in sustained yield and timber value (Crouch 1976). Damage by deer can occur on both summer and winter ranges and to both seedlings (Crouch 1976) and more mature trees (Crouch 1968, Scott and Townsend 1985, Swihart and Picone 1998). Knowing what species of conifers are preferred by local wildlife is useful when experimenting with the establishment of new conifer crops (Conover and Kania 1988) and has important forestry management implications (Rangen et al. 1994).

Understanding these kinds of plant-animal interactions may be of particular interest to foresters and urban planners considering the planting of more exotic commercial and/or ornamental species as a way to mitigate the effects of climate change or provide options for ecological restoration following wildfire or for climate change-based assisted migration planning (Rangen et al. 1994, Nigh et al. 2004, Hamann and Wang 2006). Just how targeted by herbivores exotic plants may be relative to native plants may also have implications for ecologists attempting to understand the impact of these emergent exotic ecosystems on biodiversity (Quine and Humphrey 2010) as well as for predicting, preventing, and mitigating the negative effects of biological invasions into novel habitats (Parker et al. 2006).

Recognizing that generalist herbivores such as elk and deer are known to preferentially eat exotic over native plants (Parker et al. 2006), we specifically sought to examine the winter diet choices of shelter-raised mule deer for various native and exotic conifers growing in northern British Columbia. Trials were conducted as an exploratory step to assess conifer preferences (relative consumption; see Rea et al. 2014) and as a way to determine the likelihood of damage to each species by deer in free ranges. Our null hypothesis was that deer would consume an equal amount of biomass from each species trialed, suggesting a lack of preference for one species over another.

Methods

Study Area

Tree boughs for our experiment were collected from green spaces around Prince George, British Columbia (BC), Canada (lat 53° 55' N, long 122° 46' W, 600 m above sea level) at the confluence of the Fraser and Nechako Rivers. The terrain around Prince George is flat to rolling and the landscape is covered with dense coniferous forests—hybrid white spruce and subalpine fir in the upland areas, with lodgepole pine and black spruce at lower elevations. Douglas fir here typically grows on dry, warm, rich sites (Rea et al. 2014). Prince George is on the British Columbia interior plateau and has a humid continental climate - generally wet and cool, with precipitation evenly distributed throughout the year. Mean daily average temperatures are 4.3 °C, and range from a monthly mean daily average of -7.9 °C in January, to a monthly mean daily average of 15.8 °C in July. Mean annual precipitation is 594.9.1 mm, with 205 cm of it falling as snow (Environment Canada 2016).

Plant Collections and Trial

In February of 2011, we selected 13 species of conifers in the Prince George area from which to collect boughs. The species we chose are species that are native to the interior plateau of north central BC and are used in plantation forestry or are exotic species that are commonly grown as ornamentals or have been planted experimentally in forest plantations. Northern mule deer feeding on conifers in winter, will be feeding on and impacting those species we selected for our study to various degrees. Approximately a dozen boughs were cut from 6 individuals of each of the following species: lodgepole pine (*Pinus contorta* var. *latifolia*), Scots pine (*Pinus sylvestris*), subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii* var. *glauca*), hybrid white spruce (*Picea engelmannii* x *glauca*), Norway spruce (*Picea abies*), Mugho pine (*Pinus mugo*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), common juniper (*Juniperus communis*), black spruce (*Picea mariana*), white pine (*Pinus monticola*), and Ponderosa pine

(*Pinus ponderosa*). Boughs were taken from mature trees, and cut at between 3–4 m above the ground (except juniper) using a long pruning clipper. Boughs were cut from the lower portions of each tree crown, but above the browse line to avoid collecting materials that might have been previously browsed by local ungulates. Scots and Mugho pine as well as Norway spruce are not native to northern BC and were taken from mature trees growing in green spaces such as nature parks and trail systems, as were all trees used in the trial. We did not age the trees from which we clipped boughs, but all trees were mature (cone bearing) with diameters at breast height between 30 and 50cm.

All boughs were clipped at ~ 40 cm back from their leader terminus at a diameter of ~ 1 cm, but varied somewhat according to plant architecture. Boughs were brought back to an outdoor lab facility for processing. Processing involved homogenizing materials by hand-mixing boughs from different individual trees within a species then separating materials into piles of the same species. Browse biomass was divided up so that all feeding piles were of approximately the same size (volume) resulting in 3 piles of browse for each species. Subsequent to dividing piles, materials were weighed to the nearest gram and recorded as green weight biomass for each pile separately, then labelled and packaged in large plastic bags for transport.

All browse was transported in bags at ambient temperatures (–9 °C to –20 °C) on February 18, 2011 to the Northern Lights Wildlife Shelter in Smithers, British Columbia, Canada (54°51'00.63"N 127°05'47.16"W, 680m asl) for feeding trials with human-habituated mule deer. Deer at the shelter are a mix of mule deer from throughout northern BC that were raised as orphans at the shelter (which had been rehabilitating deer for 25 years) along with their descendants and, therefore, represent genetic stock from throughout northern British Columbia.

Three piles of browse of each conifer species were haphazardly distributed on the ground (Figure 1) in an open field near the feeding yard and salt blocks where deer had been raised. We

specifically tried to control for any positional bias in the pile distribution by ensuring that boughs of all tree species were represented by piles closer to (~ 20m) and further away from (~ 25m) the feeding and salting stations. The identity of each pile was recorded as piles were distributed so that biomass removed from each could be tracked. Boughs were left out for deer to forage on for 22 hours (–10 °C to –28 °C). Feeding on materials was done exclusively by 14 mule deer during the observation periods (2h in the evening and 2h in the morning). Deer that participated in the trial were a mix of healthy prime, sub-prime and yearling animals (some of which had been hand-reared at the shelter) that moved as a herd back and forth between the shelter grounds and the surrounding wilderness several times per day as part of their routine.

Based on our observations during the evening and morning hours, all members of the group appeared to participate equally in the trial, albeit keeping track of the feeding choices of individual deer was not attempted during the trial. Trail camera footage taken during experiments conducted at the shelter in the years since our study shows that deer wander from one pile to the next while feeding, leave and return to feed dozens of times over the course of a single night. Camera footage as well as personal observations also shows that deer within groups move from pile to pile as deer compete with each other for browse resources. In this particular trial, two trackways through the feeding station made by a lone moose calf at night (outside the observation period) indicate some browsing by the calf may have been possible.

At the end of the feeding trial, all left over materials were bagged up and transported back to our outdoor lab facility for weighing and to determine the number of bites taken on boughs per pile and per species. Green weight biomass consumed was calculated for each pile by subtracting the biomass of each pile at the end of the trial from the starting pre-trial biomass. We did not correct for possible losses in green weight mass due to evaporation/transpiration or sublimation because of the short amount of time that plants were left out and because similar studies at the



Figure 1. Image of mule deer from the Northern Lights Wildlife Shelter browsing (here on Douglas fir) during a conifer cafeteria-style feeding trial where volumes of conifer boughs were divided up into approximately equally-sized piles both within and between species.

shelter concluded that such losses in water mass at similar temperatures were negligible (Rea et al. 2010). All plant materials were kept at ambient winter temperatures for the entire experiment and remained sealed in bags unless being measured or distributed for feeding.

Statistical Analyses

To determine differences in the amount of green weight biomass consumed by deer and the number of bites taken from different conifer species, and specifically between exotic, commonly encountered and rarely encountered species, we used one-way analysis of variance (ANOVA; Tabachnick and Fidell 2007). Homogeneity of variances for all ANOVA comparisons were tested using a Levene's test (Milliken and Johnson 1984). A Kolmogorov-Smirnov test was used to test assumptions of normality (Gotelli and Ellison 2004). A Tukey's HSD test was used for post-hoc comparisons (Gotelli and Ellison 2004). We specified an alpha

of 0.05. All analyses were conducted in Stastica 9.0 (Statsoft 2009).

Results

Deer consumed significantly more bough biomass $F_{(1,12)} = 3.620, p = 0.0003$ from some conifer species when compared to others (Figure 2). Specifically, more Mugho pine (MP) and Scots pine (SP) biomass was browsed when compared to hybrid spruce (HS) and black spruce (BS; $p = 0.041$; Figure 2), while no statistically significant differences in biomass consumed existed between other species trialed (all $p > 0.05$). A comparison of biomass consumption from trees classified as: 1) commonly encountered by northern mule deer (Douglas fir, black spruce, red cedar, white spruce, lodgepole pine, subalpine fir, common juniper); 2) rarely, if at all, encountered by northern mule deer (white pine, Ponderosa pine and western Hemlock) and; 3) exotic (Norway spruce, Scots pine and Mugho pine), revealed that deer ate more

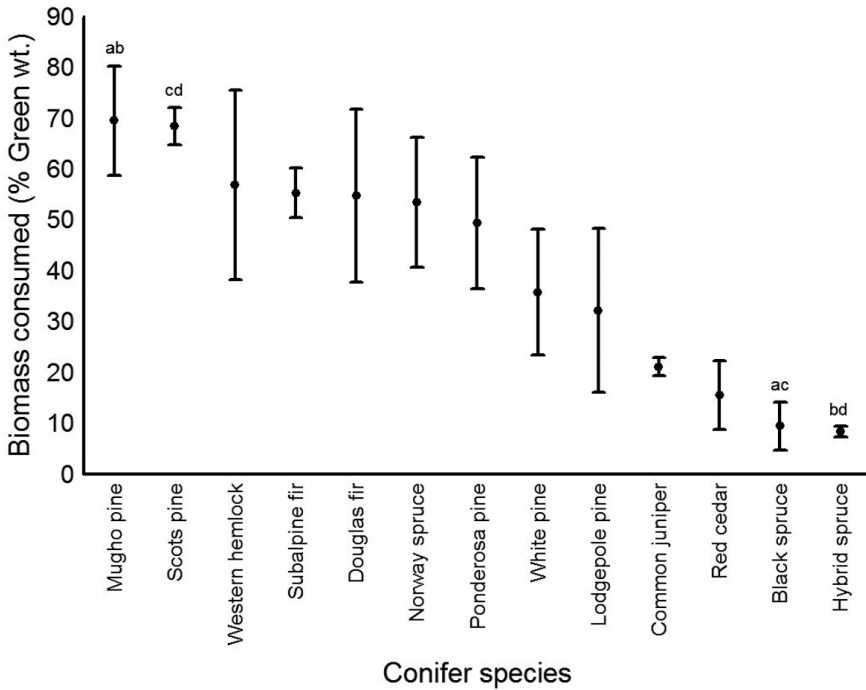


Figure 2. Mean (\pm 1SE) percent consumption of green weight conifer biomass consumed by mule deer ($n = 14$) from piles ($n = 3$ of each species) of boughs set up for a cafeteria-style feeding trial conducted in February 2011 at the Northern Lights Wildlife Shelter. Note: Means sharing a common superscript *are* significantly different ($F_{1,12} = 3.620, p = 0.0003$) from one another as determined by Tukey's HSD post-hoc comparisons.

exotics than rarely encountered species and ate more rarely encountered species than those native species commonly encountered within the range of the deer trialed $F_{(1,2)} = 4.540, p = 0.039$ (Figure 3). Specifically, more biomass was consumed from exotic species than native species ($p = 0.039$),

while no statistically significant differences in biomass consumed existed between other groups trialed (all $p > 0.05$). A general relationship existed between the green weight biomass consumed and the number of bites taken by deer from each species trialed, which indicated that deer generally

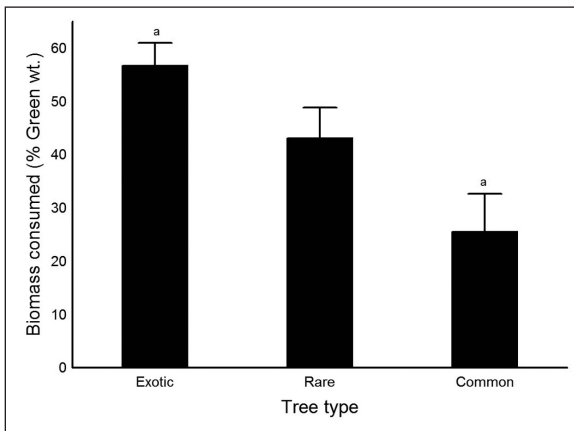


Figure 3. Mean (\pm 1SE) percent consumption of green weight conifer biomass consumed by mule deer ($n = 14$) from exotic ($n = 3$ species), North American native conifers outside the range of northern mule deer ($n = 3$ species), and native species encountered by northern mule deer ($n = 7$ species). Results are from a cafeteria-style feeding trial conducted in February 2011 at the Northern Lights Wildlife Shelter, Smithers, British Columbia. Note: Means sharing a common superscript *are* significantly different ($F_{1,2} = 4.540, p = 0.039$) from one another as determined by Tukey's HSD post-hoc comparisons.

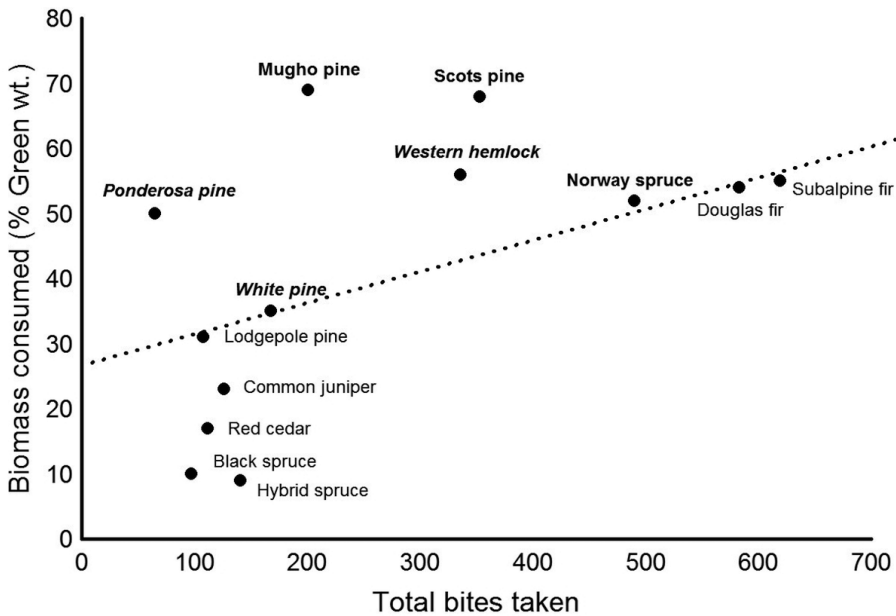


Figure 4. Relationship of the percent biomass consumed to the number of bites taken from each conifer species by mule deer during a cafeteria feeding trial conducted at the Northern Lights Wildlife Shelter in February 2011 with dotted line indicating a relationship of biomass consumed to bites taken above which deer focused on exotic (bold type) and rarely encountered native (bold and italicized type) conifer species and below which they focused on native conifers.

took more bites from exotic and rarely encountered conifers, but not always and took more total bites from commonly encountered Douglas and subalpine fir (Figure 4).

Discussion

Our feeding trial suggests that mule deer at the shelter consumed more biomass and took more bites of some species of conifers over others. Generally, the pattern we observed was one of deer eating more biomass from exotic species than those rarely encountered by deer, while commonly encountered native species were consumed less than exotic and rarely encountered species. Specifically, deer consumed significantly more biomass from exotics than from commonly encountered species and significantly more biomass from Mugho and Scots pine than from black and hybrid spruces. In addition to biomass consumption, deer also took more bites from exotic and rarely encountered conifers than from most of those species that they are more likely to com-

monly encounter (the exceptions being Douglas fir and subalpine fir; see Figure 4).

Unlike Scots pine which is native to northern Europe (but considered by some to be a minor invasive of Canada) and preferred by ungulates of that region (Gill 1992, Bergquist and Örlander 1996, Elfving et al. 2001), North American pines and spruces are considered to be of low preference for North American deer (Ullrey et al. 1967, Thompson and Euler 1987). Pine consumption in winter by Mule deer is generally considered to be minimal (Kufeld et al. 1973) with black and hybrid white spruce completely avoided or rarely browsed (Tremblay et al. 2005, Sauvé and Côté 2007). Norway spruce, which is native to much of northern Europe is sometimes eaten (Heikkilä et al. 2003, Lykke 2005), but generally avoided by native European ungulates (Bergström and Hjeljord 1987). When grouped with other exotic species in our trial, however, Norway spruce was consumed significantly more by mule deer (with 5 times as many bites taken) than native black and

hybrid spruces. Together, these findings suggest a preference by deer for exotic over commonly encountered native conifers.

Although deer generally consumed more biomass and took more bites from exotic and rarely encountered conifers than commonly encountered species, deer did take the most bites (but not biomass) from Douglas fir and subalpine fir. Interestingly, these two species (especially Douglas fir) are important to northern mule deer and make up a significant proportion of their winter diets in British Columbia (Willms et al. 1976, Dawson et al. 1990, Armleder et al. 1994, Hodder et al. 2013) and elsewhere within mule deer range (Kosco and Bartolome 1983).

Why mule deer may have selected certain species of conifers over others is complex and is likely related to the nutritional value of the browse (including chemical defenses), and twig morphometry (Hanley 1997, Shipley et al. 1999, Cappuccino and Arnason 2006) as well as previous browsing experience. Deer living at the shelter have continuous access to the wilderness surrounding the shelter after 6 months of age. As such, deer have access to dozens of native deciduous browses along with lodgepole pine, subalpine fir, hybrid spruce, black spruce, common juniper, Douglas fir and occasionally red cedar at the edge of the range and where it has been used in plantation forestry and as an ornamental. Ponderosa pine, white pine, and western hemlock, while native to northern BC, grow outside of the range of deer at the shelter and would be seen as novel food items, as would the exotic Mugho pine, Scots pine, and Norway spruce.

Novelty may be suggested as a reason why deer in our trial may have selected what they did (with the exception of subalpine fir and Douglas fir), and is in fact supported by several studies highlighting the fact that native, generalist herbivores like deer preferentially attack exotic over native plant species (Parker et al. 2006). Where exotic deer are concerned, however, trends may be reversed (Nunez et al. 2008). Understanding the tree species affected by deer has important implications for plantation and urban forestry where deer damages can be severe and costly and

mitigation measures must be developed (Crouch 1976, Rangen et al. 1994).

According to the Biotic Resistance Hypothesis (Elton 1958), exotic species are ill-equipped to defend themselves against novel herbivores found within introduced ranges (Levine et al. 2004). Consequently, the Biotic Resistance Hypothesis predicts a preference of mule deer used in our trial for European over native North American conifers. At the same time, high levels of co-adaptation may help to explain the continued importance (in terms of bites taken) of native firs to northern mule deer (Hanley et al. 2007).

Conclusions

Although determined through a short-term feeding trial, our findings do suggest that when given equal access to a variety of conifers, northern mule deer will browse exotic Mugho and Scots pine over native black and hybrid spruce and in general appear to prefer exotic over native conifers. Our trial, like other feeding trials with mule deer (Schwartz et al. 1980, Welch et al. 1983, McArthur et al. 1993) should be considered exploratory and somewhat artificial. Free-ranging deer must consider many factors not present in trial conditions while selecting trees on which to browse. Such factors include mineral and allelochemical content and the nutritional cost/benefit decisions that must be made in addition to factors influencing foraging itself (McArthur et al. 1993).

Firm conclusions regarding the preferences we determined here cannot be drawn without controlling for variables such as genetic strains, geographic sources, site-specific growing conditions, moisture and light availability and until additional trials with larger sample sizes have been conducted. Because short and long term preferences by deer may vary (Relva et al. 2010), longer term cafeteria-style and field trials using more replicates within and across different ranges should be conducted. In the meantime, we contend that our trial may help guide foresters and urban planners experimenting with which trees to plant in settings such as parks and tree farms and how, based on whether or not they are exotic, they may be impacted by local deer.

Because the consequences of these unique plant animal interactions may impact biodiversity at multiple levels (Quine and Humphrey 2010) and may influence biological invasions of native habitats (Parker et al. 2006, Nunez et al. 2008), herbivore preferences for various plantation crops should be considered by more than just urban and plantation foresters contemplating the use of exotic species.

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