The Effects of Lactation on Seedling Damage by Mountain Beaver

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ABSTRACT: The mountain beaver is a semi-fossorial rodent of the Pacific Northwest and is among a variety of herbivores that retard plant growth and cause tree seedling deformities and mortality. Douglas-fir seedlings are planted in the Pacific Northwest from February through March, a period coinciding with mountain beaver parturition. Previous research suggested that in spring, lactating females depend more on conifers than do non-lactating females and males. We conducted experiments to determine if female reproductive condition influenced seedling damage, and if physiological stage of the seedling affected damage. Dormant and flushing trees were offered to 6 pregnant and 6 non-pregnant females in 2002 and 2003. We found no difference between female condition and damage in 2002, but there was a significant difference between type of tree and damage ($F_{6,79} = 6.75$, $P < 0.001$). In 2003, we found a difference in seedling damage ($F_{3,95} = 16.41$, $P < 0.001$), with tree type ($P < 0.001$) and female condition ($P = 0.02$) contributing to the model. More flushing trees were damaged in both years than dormant trees, once bud break occurred. Statistical analyses of fructose ($F_{5,23} = 12.07$, $P < 0.001$) and glucose ($F_{5,23} = 12.86$, $P < 0.001$) concentration data indicate that tree type (dormant or flushing) was a significant effect ($P < 0.001$). The interaction between tree type and week sampled was also significant in both the glucose ($P = 0.002$) and fructose response ($P = 0.009$). Both fructose and glucose concentrations were the lowest in new flushing trees, and mountain beaver did not appear to be selecting flushing trees for their needle sugar content. Water concentration also varied between tree type but was not affected by the sampling time ($F_{5,20} = 35.46$, $P < 0.001$). New and dormant growth tissues had similar water concentrations that were greater than old growth tissue. Mountain beaver are dependent upon a constant water source, although it dose not appear that damage is related to water availability. Further analyses of terpene levels and stem carbohydrate levels are needed before conclusions on mountain beaver selectivity can be reached.

KEY WORDS: *Aplodontia rufa*, carbohydrates, damage, Douglas-fir, lactation, mountain beaver, seedling, terpenes

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INTRODUCTION

Mountain beaver (*Aplodontia rufa*) are primitive, fossoril rodents with a limited geographic distribution extending from southern British Columbia south to central California and east to the Cascade and Sierra Nevada ranges. Although mountain beaver can be found up to 2,200 m elevation in portions of the Sierra Nevada, they are more commonly found at lower elevations in humid, densely vegetated understory areas (Walker et al. 1975, Feldhamer and Rochelle 1982). Mountain beaver densities are related to stand opening and can increase from <4 animals/ha to greater than 6 - 7 animals/ha after harvest (Neal and Borrecco 1981). Because of this tendency to seek stand openings, recently planted clear-cuts offer an attractive habitat for dispersing mountain beaver. Borrecco and Anderson (1980) documented that the majority of recorded mountain beaver damage occurred from the Olympic Peninsula to the Puget Sound Trough and the Coast Range to the Willamette Valley, with very little damage occurring in northeast California. In a 1977 survey, over 111,000 ha in the Pacific Northwest– 75% of that in Douglas-fir (*Pseudotsuga menziesii*) stands alone– was damaged by mountain beaver (Borrecco et al. 1979). The most severe damage occurred immediately following, and up to 4 years after, planting and resulted in seedling mortality or plantation failure (Borrecco et al. 1979, Feldhamer and Rochelle 1982). Due to the impact on seedling plantation, mountain beaver are managed as a pest species in both Oregon and Washington.

Douglas-fir does not appear to be a highly preferred forage of mountain beaver, yet establishment of Douglas-fir seedlings is often difficult in areas with mountain beaver. Mountain beaver are described as voracious in their dietary habits (Godin 1964, Valadka 1988), with the predominant criteria for plant selection being availability (O'Brien 1988, Valadka 1988). In addition, some mountain beaver demonstrate forage preference (Nolte and Arjo, unpubl. data). Plants toxic to other herbivores (i.e., *Delphinium glaucum*, *Pteridium aquilinum*) are often ingested by mountain beavers (Voth 1968, Muenscher 1975, O'Brien 1988). Although sword fern (*Polystichum munitum*) and salal (*Gaultheria shallon*) are clipped year-round as a food and bedding source (Neal and Borrecco 1981), these food sources have relatively low energy content, forcing the mountain beaver to spend approximately 75% of its active time gathering and ingesting food (Ingles 1959).

Optimal foraging theory predicts that animals minimize their foraging energy expenditure while maximizing their energy intake in the choice of forage (Stephens and Krebs 1986). Voth (1968) documented that lactating female diets differed from male diets, with the former consuming more conifers. His conclusion was that females were choosing Douglas-fir seedlings in the spring when protein content and nutritional demands

were high. Kimball et al. (1998) showed that black bears (*Ursus americanus*) selectively forage on trees in spring to maximize their carbohydrate intake but at the same time minimize their terpene intake. Douglas-fir seedlings are planted in the Pacific Northwest from February through March, a period coinciding with mountain beaver parturition. If damage to seedlings is caused predominantly by lactating females, it may be possible to selectively target one sex of the species (i.e., through contraceptives) to reduce seedling damage. We conducted a study to increase our understanding of mountain beaver biology and behavior in order to assist managers in developing more effective approaches to control mountain beaver damage. Our specific objectives were to 1) determine if lactation affects seedling damage, and 2) determine if damage to seedlings is dependant upon growth stages of the seedlings.

METHODS

Mountain beaver were already established in habitat pens measuring 11 × 16 m at the Olympia Field Station, prior to the start of the study in 2002. Each habitat pen contained a nest box for each of the 2 animals, located at opposite corners of the enclosure. A nest boxes consisted of a 76-liter trash can buried in the soil with an exit to the surface through a 1.5-m corrugated pipe (10 cm in diameter). Opposite the exit pipe was a 0.5-m corrugated pipe buried in the soil to facilitated natural burrowing by the animals. An A-frame roof covered each nesting structure. A common feed station and water bowl were located in the middle of the enclosure, and subjects had free access to water, apple, and lab rodent diet in their pen throughout the study. Straw for bedding and alder branches for gnawing were provided weekly. We live-trapped all pens in March 2002 to remove males and to determine reproductive condition of the females through palpation. Traps were deployed for 1 week, at which point we no longer captured any new animals and we assumed all animals had been removed. Six pregnant females and 6 non-pregnant females were left in the habitat pens for the study.

For the 2003 study, 24 adult mountain beavers (12 males and 12 females) were live-captured in Grays Harbor County, Washington, and established in the same habitat pens at the NWRC Olympia Field Station. Animals were individual marked with AVID microchips (American Veterinary Identification Devices, Norco, CA) and ear tags. Pairs were placed in habitat pens in December 2002 and early January 2003. Breeding season for mountain beaver usually occurs from the end of January to the middle of February. In March, we trapped each habitat pen to remove the males and check on the condition of females. Six pregnant females were left in the habitat pens. In addition, 6 females established in indoor pens were used as the non-lactating individuals. These animals were originally penned individually in covered pens (3 × 3 m) that each contained a simple artificial nest structure. Each nest structure consists of three 76-liter cans with lids, connected with perforated plastic pipe (10-cm diameter). Subjects had free access to water and apple in their pens throughout the study. Lab rodent diet was not offered during the 2003 study because of concern that the high carbohydrate content of the diet might bias selection of trees. Mountain beavers were provided straw to build nests. Two weeks prior to the start of the study, the non-lactating females were introduced to habitat pens for acclimation.

Vegetation in habitat pens varied from a "complex" to a "medium" to a "barren" vegetation regime. The "complex" regime contained groups of salal, sword fern, and Oregon grape (*Berberis nervosa*), 12 large (>1.5-m) and 6 small (<0.5-m) individual red huckleberry (*Vaccinium parvifolium*) plants, and cat's ear (*Hypochaeris radicata*) rosettes located throughout the enclosure at 1-m intervals. Huckleberry and cat's ear are present in the "medium" regime as described in the "complex" regime; however, the other plants are not present. The "barren" regime contained no plants other than 4 alder (*Alnus rubra*) shade trees, although some cat's ear was growing in places. In both years, each female was allowed access to 2 adjacent habitat pens during the study to prevent any bias in available vegetation. Addition salal branches were provided weekly.

Seedling Damage Assessment

In 2002, 48 Douglas-fir seedlings (2-0 stock) were planted in 12 of the habitat pens containing the nest site for females the last week of March. Seedlings were planted 1 m apart in 8 × 6 rows. Six of the seedlings were dormant trees and were randomly assigned a position in the grid. In addition, 6 flushing trees were planted in random positions. The remaining trees (non-test trees, n = 36) were planted from the dormant stock the first week.

We determined that sample size was not adequate during 2002, so we increased the sample size of test trees in the 2003 study. Forty-eight Douglas-fir seedlings (2-0 stock) were planted in 8 × 6 rows the first week of April. Twelve seedlings were dormant trees and 12 seedlings were flushing trees; the remaining 24 trees were non-test trees.

We assessed damage twice a week in each pen. The height of damaged trees was measured and damaged trees were replaced each Friday. Dormant trees were changed every week, with or without damage, to maintain dormancy. Those trees not designated as test trees, and flushing test trees with damage, were replaced with flushing trees from a nearby nursery when necessary. We conducted this study for 10 weeks in 2002 and 12 weeks in 2003. An analysis of variance (SAS® Version 8.0, SAS institute Inc., Cary, NC) was used to test for differences in damage between pregnant and non-pregnant females, types of tree (dormant or flushing), and week, for each year. Sampling dates were converted to a continuous variable (22 March 2002 or 9 April 2003 – Week 1) for analyses.

Carbohydrate Analyses

Carbohydrate analyses were conducted on both flushing and dormant trees in 2003. Five lateral clippings from 3 dormant trees were sampled each week. In addition, we sampled 5 flushing trees from the field. Clippings from 5 new candles and 5 previous-year-growth laterals were used for the analyses. Each sample was vacuum-sealed and stored in a conventional freezer

until processing. Needles were removed from lateral stems and homogenized in liquid nitrogen with an automated freezer mill. Samples of ground needles were then vacuum-sealed and returned to the freezer until further analyses. Quantitative methodology for determining soluble carbohydrates in conifer needle tissue after emergence of new growth (bud break) followed Kimball et al. (2004). Differences in each carbohydrate response and water were analyzed using a one-factor analysis of variance with week as a covariate. Tissue types (dormant, previous-year, or new) were factors in the analyses.

RESULTS

2002 Seedling Damage

Trees were planted on 22 March 2002 and were monitored through 24 May 2002. Buds were first noted on 26 April, and the trees were fully flushing by 17 May. We used only 8 of the 12 females for the damage analyses, since males were recovered at the end of the study in 4 pens (2 with pregnant females and 2 with non-pregnant females). Juveniles were captured with 2 females (Pen #4 – 2 males and Pen #19 – 3 males). In addition, the female in Pen #16 also had 2 pups but lost them both when she was disturbed in early April. Seedling damage differed significantly by type (dormant or flushing) of tree ($F_{6,79} = 6.75$, $P < 0.001$) but was not dependant upon condition of the female or week. None of the interactions between factors was significant. When seedlings started to flush around Week 5, damage to dormant trees decreased, while damage to flushing trees increased (Figure 1). Since the female in Pen #4 was one of the few females who successfully raised a litter, we reanalyzed the data to include her and another non-pregnant female (also with an additional male); however, results were similar. Damage per week varied between females and even within female reproductive condition. The pregnant female in Pen #17 damaged less than 2 trees per week, and after week 6 she did not damage any seedlings. Other pregnant females, such as one in Pen #13, damaged up to 31 trees during week 6. Juveniles were unlikely to have contributed to the damage at this time, since they were still probably too young to leave the nest. All of the non-pregnant females contributed weekly to seedling damage. The female in Pen #5 damaged between 12 and 44 trees per week.

2003 Seedling Damage

We not only increased the sample size of the test trees in 2003, since females easily damaged up to 45 trees per week, but we also monitored trees longer. Seedlings were planted 9 April and monitored through 25 June. Flushing occurred at Week 5. Unlike the 2002 study, we recovered no juveniles during 2003. Three of the "pregnant" females captured in June did have dark hair around their nipples, indicating prior lactation. Damage results were similar to the 2002 study, where damage to dormant trees decreased while damage to flushing trees increased after Week 5 – flushing (Figure 2). Only 6 females were used in the analyses. One non-pregnant female died in her pen during Week 5, and 2 other non-pregnant females (Pens #16 and #8) were not recaptured at the end of the study. No damage occurred in these pens after Week 1 and Week 6, respectively. Both of these females likely perished. In addition, 2 pregnant females were not recaptured at the study completion (Pens #14 and #15). These pens were adjacent to Pen #13, and the pregnant female from this pen was found to be using both her pens and the adjacent Pen #14. We therefore also did not use her in the analyses. We found a difference in seedling damage ($F_{3,95} = 16.41$, $P < 0.001$), with tree type ($P < 0.001$) and female condition ($P = 0.02$) contributing to the model. Non-pregnant females damaged more seedlings than pregnant females. Weekly damage varied between females and even within reproductive condition. The pregnant female in Pen #4 never damaged more than 1 tree a week, whereas Female #18 damaged between 2 and 26 seedlings per week. The non-pregnant female in Pen #23 damaged a large amount of seedling after Week 1– up to 33 in 1 week.

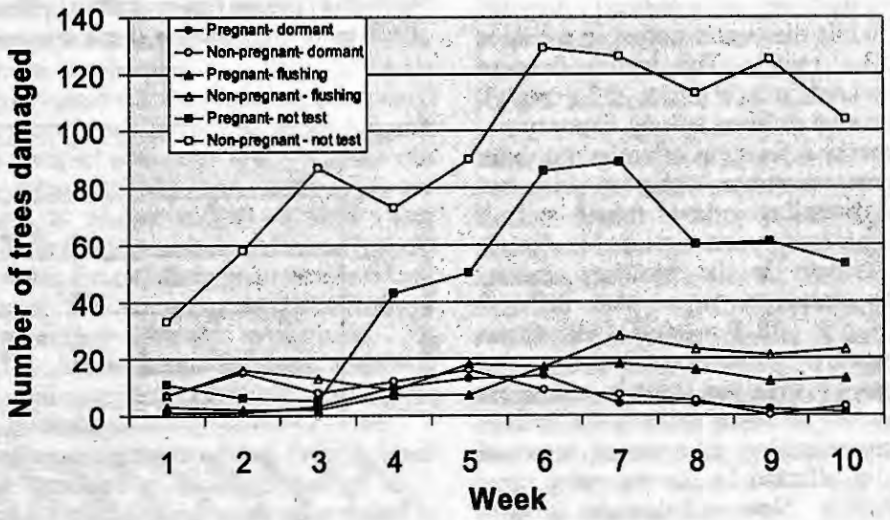

Figure 1. Douglas-fir seedlings damaged by pregnant and non-pregnant female mountain beaver in 2002. Seedlings were classified as dormant, flushing, and non-test trees.

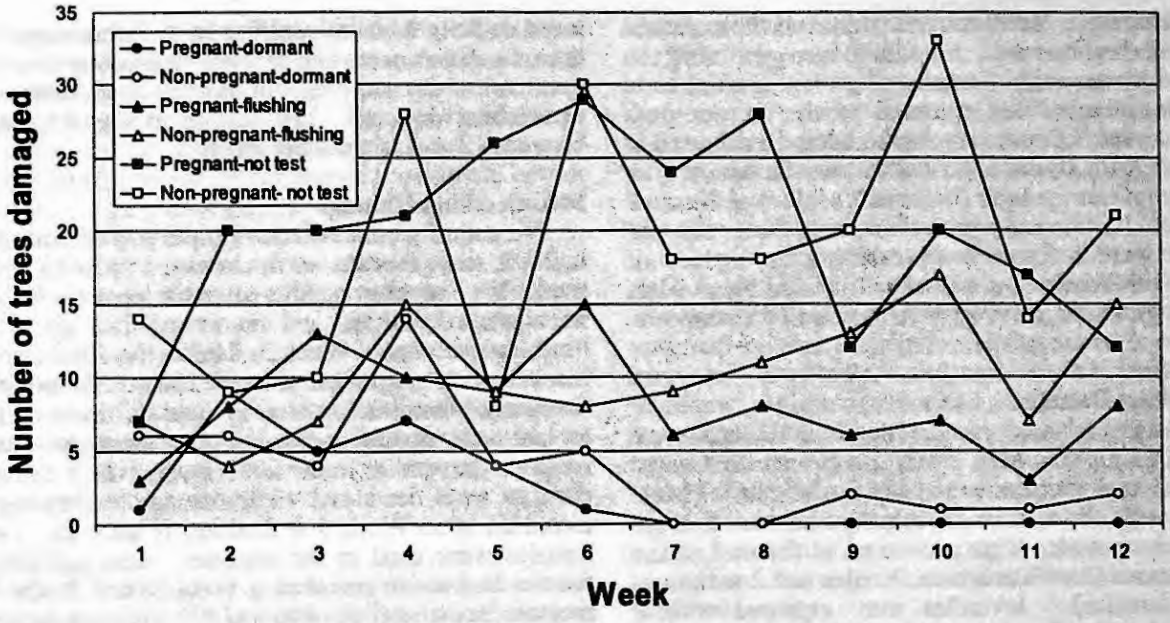

Figure 2. Douglas-fir seedlings damaged by pregnant and non-pregnant female mountain beaver in 2003. Seedlings were classified as dormant, flushing, and non-test trees.

Carbohydrate Analyses

Three carbohydrates were found in significant quantities in the needle samples: fructose, glucose, and an unknown sugar. This unknown sugar is likely a deoxy monosaccharide, and future identification is pending. Statistical analyses of the fructose ($F_{5,23} = 12.07$, $P < 0.001$) and glucose ($F_{5,23} = 12.86$, $P < 0.001$) concentration data indicate that the covariate (week) was not significant for either response, while tree type (dormant or flushing) was a significant effect ($P < 0.001$). However, the tree type × week interaction was also significant in both the glucose ($P = 0.002$) and fructose response ($P = 0.009$). Sugar concentrations differ among tree types, regardless of the week they are sampled (Figure 3 and 4). Mean fructose concentration in dormant tissue was 17.3 mg/g, while the concentration in previous year's growth was 21.1 mg/g. The lowest fructose concentration was observed in new tissue (12.8 mg/g). Glucose concentrations also differed among tissue types. However, differences were a function of sampling time. While the glucose concentration was highest in previous-year's growth at each sampling interval (mean = 16.3 mg/g), glucose was higher in dormant tissues at budbreak and higher in new growth in the growing season. Concentrations of the unknown sugar also differed between tissue types ($F_{5,23} = 7.08$, $P = 0.004$), with tissue type ($P < 0.001$) and week ($P = 0.02$) contributing to the model. Dormant tissue contained higher unknown carbohydrate concentration, and new growth the lowest (Figure 5). Water concentration also varied between tissue types but was not affected by the sampling time ($F_{5,20} = 35.46$, $P < 0.001$). New and dormant growth tissues had similar water concentrations that were greater than old growth tissue (Figure 6).

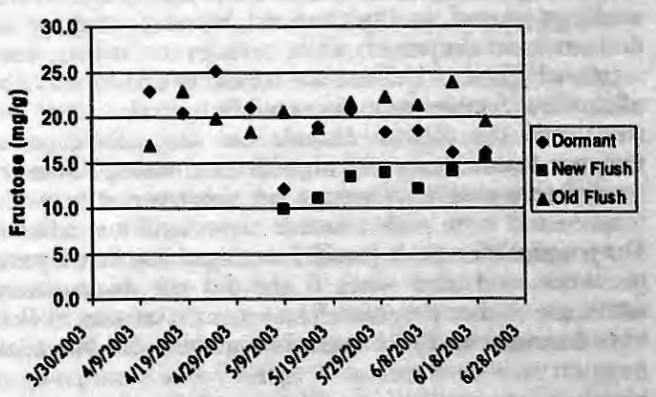

Figure 3. Fructose concentration in Douglas-fir tissue. Each point represents a single composite sample.

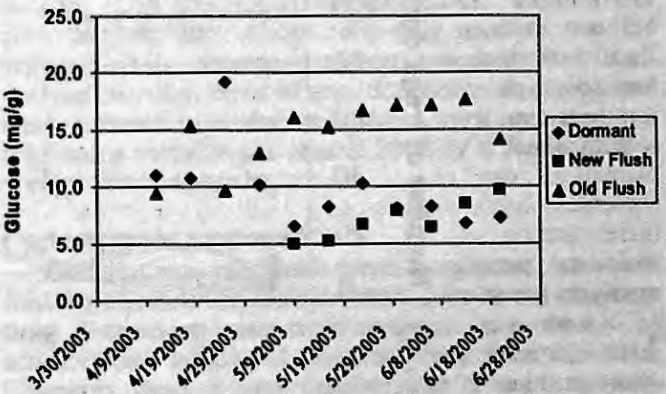

Figure 4. Glucose concentration in Douglas-fir tissue. Each point represents a single composite sample.

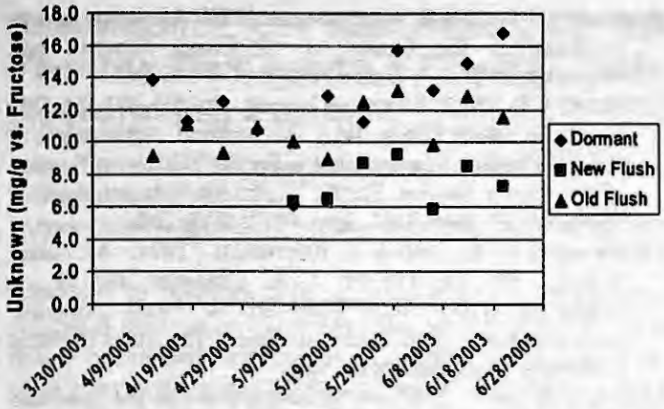

Figure 5. Unknown sugar concentration in Douglas-fir tissue. Each point represents a single composite sample.

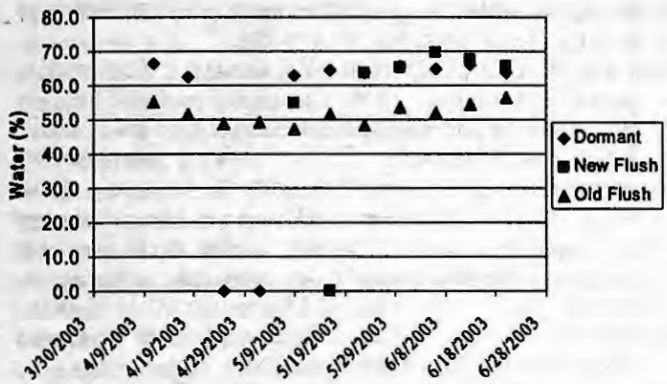

Figure 6. Water concentration in Douglas-fir tissue. Each point represents a single composite sample.

DISCUSSION

Mountain beaver can inflict a variety of types of damage to timber resources on both young and older trees, above and below ground (Cafferata 1992). The most prevalent injury, however, is the clipping of young seedlings immediately after planting (Hooven 1977, Borrecco et al. 1979). Mountain beaver at higher elevations in the Sierra Nevada remove limbs and bark from conifers between September and May (O'Brien 1988). O'Brien (1988) reported that conifers comprised 100% of the caches observed from December through February, although sample size was low. Unlike the Pacific Northwest where sword fern and salal are available year round, at higher elevations little other forage is available to mountain beaver. However, even with availability of some forage, damage to new seedling plantations can occur. Since planting of seedlings coincides with mountain beaver parturition, an understanding of the relationship between the two biological periods and seedling damage may assist managers in reducing damage.

In a series of feeding experiments, Voth (1968) noted several observations concerning mountain beaver food selection: 1) lactating females depend more on conifers in the spring than non-lactating females and males, 2) lactating females have a diet with high water content, 3) Douglas-fir needles and not stems were ingested, 4) no Douglas-fir clippings were found in outside caches, and 5) a very low proportion of conifer was found inside 4 food chambers. More epidermal fragment counts for Douglas-fir was observed in lactating females (Voth 1968); however, sample size was small (n = 3). Managers have then extrapolated from these data to conclude that female mountain beaver may cause more damage on newly planted units. In this study, we found no difference in seedling damage between lactating females and non-lactating females in either year. One problem with trying to conduct this type of experiment is the uncertainty of whether females are able to successfully raise their litters. Once we introduced animals into the habitat pens, we had no way to be sure litters would be raised to weaning. Mountain beaver tend to be easily stressed and will often kill their young under stressful situations. Even with minimizing the disturbance in the habitat pens, complications may still have arisen. We did have half of the females in 2002 successfully give birth, but we still did not see a difference in tree damage related to female reproductive condition. Damage appears to be very individualistic, even with available alternative forage.

The mountain beaver has the distinction of being the most primitive member of Rodentia (Borrecco and Anderson 1980). The physiological constraints associated with primitiveness limits their geographical range to humid temperate climates. Due to their inability to concentrate urine, mountain beaver require a large daily intake of water (Pfeiffer et al. 1960). We did not find that mountain beaver were choosing seedlings based on water content. Although new growth tissue had higher water content than the old growth, water content was similar to the dormant tissue, yet mountain beaver did not selectively forage on dormant trees once flushing occurred. Water was provided continually throughout the study, so at no time were animals water stressed.

Although we did not demonstrate that lactating females inflicted more damage than non-lactating females, we did note a significant change in damage related to tree type. Voth (1968) originally hypothesized that females were choosing seedlings for an increase in protein content, and then switched to grasses and forbs when their protein content increased. Kimball et al. (1998) demonstrated that vascular tissue from Douglas-fir trees in the spring offers a high energy diet during a relatively scarce foraging period. Foraging experiments indicated that bears preferred high carbohydrate and low terpene diets. Greater accumulations of carbohydrates during winter have been noted in temperate zone gymnosperms (Kozlowski and Keller 1966 cited in O'Brien 1988). Mountain beaver may be selecting seedlings for similar reasons, even though salal and sword fern are still present. Females in this study switched from foraging on both dormant and flushing trees to selecting only flushing trees once bud break occurred. Results from the needle tissue samples showed that sugar content in new flushing needles was less than in old tissue and even in dormant tissue. If mountain beaver were selecting trees for higher sugar content, then selection for dormant trees should have continued.

Ferns are a primitive species that are more easily masticated, and presumably digested, because of the increased tissue boundaries (Voth 1968). Parker et al. (1999) documented that from December to June ferns increased in amount of digestible energy available to black-tailed deer (*Odocoileus hemionus*). Each year, 5 females damaged >100 seedlings during the study. In 2003, these numbers were 4 times greater than the damage incurred in other pens. Nolte and Arjo (unpubl. data) documented that seedling damage decreased when mountain beaver had access to preferred forage. Two of the females with the most damage in each year were located in "medium" regime pens, whereas the other females had access to "complex" regime pens. Even though the "complex" regime pens contained sword fern, it does not appear that the availability of a preferred forage influenced damage between these pens. Forty-eight seedlings covered almost the entire pen, and it may just be a matter of quantity of availability (additional non-test trees), and perhaps the increase in caloric reward at minimal foraging effort, that influenced the preference for foraging on seedlings compared to sword fern. In 2002, several females, both lactating and non-lactating, damaged a considerable number of non-test trees (Figure 1). The availability of non-test trees in comparison to test trees, in addition to the position within the grid of the test trees (i.e. distance to nearest burrow opening), possibly influenced the seedlings "chosen" by the mountain beaver and may have influenced our results.

Although Voth (1968) documented mountain beaver not foraging on conifer stems, this is the part of the tree that mountain beaver "test" before foraging. One female consistently had peeled stems from the seedlings in front of her nest opening. Carbohydrate levels may be different in the stems versus the needles, and the mountain beaver are therefore choosing trees based on the carbohydrate concentrations in the stem. In addition, we did not analyze the tissue for secondary compounds such as terpenes. Zou and Cates (1995) document an increase in volatiles during the growing season as carbohydrate levels decrease. Mountain beaver may be selecting seedlings with a low terpene-to-carbohydrate ratio instead of just the simple sugars. An analysis of both stem tissue and terpene concentrations is needed before further conclusions on mountain beaver selection can be made.

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