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Mule Deer (Odocoileus hemionus) in central and northern British Columbia forage on the boughs of conifers such as Douglas-fir (Pseudotsuga menziesii; Waterhouse and others 1991, 1994), and less frequently, Subalpine Fir (Abies lasiocarpa; Hodder 2009) in winter. Conifer seedlings and saplings are eaten, but Mule Deer prefer to feed on boughs from the canopy of more mature trees (Armleder and Dawson 1992). Top branches of conifers are thought to be less chemically-defended and of higher nutritive value than those growing within the reach of browsers (Swihart and Picone 1998), but are generally inaccessible. Access to mature tree tops is often believed to be limited to tree toppling events, limb breakage, and logging, and is episodic (Waterhouse and others 1991).

American Red Squirrels (*Tamiasciurus hudsonicus*; hereafter Red Squirrels) commonly clip the current annual shoots (tips) off of conifer canopy branches that contain overwintering and nutrient-laden buds and cones (Eder and Pattie 2001). Once clipped, the foliage drops to the ground where Red Squirrels can immediately forage on buds or cones or collect and cache the forage in nearby middens for later use (Fig. 1; Elliott 1988).

During several years of field work on a Mule Deer winter range in central British Columbia, we observed that Douglas-fir clippings from Red Squirrels are commonly found carpeting the snowy forest floor in mid to late winter. Microhistological analyses of Mule Deer fecal pellet samples collected in the area have revealed that winter pellets of deer comprised more than 91% conifers (63%) and shrubs (29%), with 48% of the conifer fraction being Douglasfir needles (Hodder 2009).

To determine the potential forage biomass for Mule Deer contributed to the forest floor by Red Squirrels, we estimated the mass of branch tips clipped and dropped to the ground by Red Squirrels between mid to late winter, when Mule Deer are most likely to encounter and forage upon this potential food source.

Our study was conducted within the John Prince Research Forest (UTM Zone 10: 408300E, 6056500N, WGS84), near Fort St. James, British Columbia, Canada. The area is characterized by rolling terrain with low mountains (700 m to 1250 m asl). The overall mean daily average temperature is 3.1° C, with a mean daily average temperature of -11.3° C in January and 15.3° C in July. Mean annual precipitation at Fort St. James is 487 mm, with 192 cm of snowfall (Environment Canada, unpubl. data).

While the stands that represent Mule Deer winter range are predominantly (>50%) Douglasfir, there also tends to be a large component of Lodgepole Pine (*Pinus contorta* var. *latifolia*) and hybrid White Spruce (*Picea glauca* × *engelmannii*) within these stands. There are approximately



FIGURE 1. Red Squirrel amidst Douglas-fir bough clippings (top) and Human-habituated Mule Deer (bottom) foraging on Douglas-fir twigs that we clipped to simulate squirrel clippings. Both photos were taken at the Northern Lights Wildlife Shelter, Smithers, British Columbia. (Photos: Roy Rea).

14,000 ha of forested area in the region that meets the definition of Mule Deer winter range; which is coarsely defined as south-facing Douglas-firdominated stands (Sulyma and Vinnedge 2003).

To determine potential forage biomass contributed to the forest floor by Red Squirrels, we collected all Douglas fir clippings on the ground in twelve, 9.77-m radius plots. Because our observations indicated that Red Squirrels clipped Douglas-fir branch tips more intensively near middens, we located the majority (n = 9) of these plots at the middle of active Red Squirrel middens. We also established 3 plots in areas adjacent to middens. Litterfall was collected within these plots in mid-February 2004 and then again in mid-April 2004.

We meticulously checked each plot and removed all clippings present on the forest floor above the snowpack. Our plots were located in winter range areas where forest cover is substantial (>70% canopy cover) and snow pack was relatively shallow (<10 cm on average). Nevertheless, we may have missed some twigs clipped by squirrels.

Clippings were immediately weighed fresh (wet) in the lab. We assessed each individual twig collected in February, determining the wet twig mass, twig length and twig basal diameter. From these data, we developed and present regression equations for each possible combination of twig morphometric variables. To test differences in the amount of biomass collected within the sample plots between the February and April collections, we used a Repeated Measures Analysis of Variance. All statistical tests were performed in Statistica (ver. 6.0, Statsoft Corporation, Tulsa, OK).

We used equations developed by Waterhouse and others (1991) to estimate the number of Mule Deer/day/hectare that could be supported by twig biomass on the ground that was contributed to our study plots by Red Squirrels.

To confirm that Mule Deer eat clippings from the upper branches of Douglas-fir trees, we pruned large branches from 10 Douglas-fir trees in known Mule Deer winter range near Prince George, British Columbia in February 2009. Branches were cut at approximately 10 m above the ground. We then clipped approximately 300 twig tips from branches to dimensions similar to those we had earlier taken and measured from our plots. We offered these clippings to 13 Mule Deer, 1 Elk (Cervus elaphus), and 3 Moose (Alces alces) housed at the Northern Lights Wildlife Shelter in Smithers, British Columbia (approximately 400 km west of our study area). The clippings were haphazardly scattered on the forest floor near the feeding station at the shelter, after which we observed approximately how many twigs were consumed by each ungulate, with specific attention being paid to Mule Deer forage choices (Fig. 1.).



FIGURE 2. Mean $(\pm s_{\overline{\chi}})$ twig biomass collected in mid-February and mid-April 2004 from 9.77-m plots within squirrel midden areas (n = 9) and control areas (n = 3) in a core Mule Deer winter range in the John Prince Research Forest, British Columbia.

We collected 803 twig clippings in the plots in February 2004. The mean biomass of twig tips was 2.78 g, (s = 6.23 g) with an average twig length of 11.18 cm (s = 9.15 cm) and a woody stem basal diameter of 2.3 mm (s = 1.1 mm). The average total biomass that was contributed to the forest floor in February was 6.3 kg/ha (s = 5.3 kg/ha) in midden plots and 5.5 kg/ha (s = 7.2 kg/ha) in control plots, and in April was 60.7 kg/ha (s = 44.3 kg/ha) in middens and 46.1 kg/ha (s = 41.7 kg/ha) in controls. Because Red Squirrels only clip branch tips, we considered all clippings to be dropped by squirrels with the exception of about 12% of the boughs that appeared to have been broken rather than clipped. Total twig biomass varied between collection periods, but was not significantly different (F [1, 4] = 2.654, P = 0.179) between control and midden plots within either collection period (Fig. 2). Regression equations of twig morphology indicated positive significant relationships between twig mass, base diameter, length, and width (Table 1; Fig. 3).



FIGURE 3. Relationship of twig length to twig diameter for Douglas fir clippings of Red Squirrels collected in central British Columbia, February 2004.

Based on 14 kg wet weight of branch clippings contributed to the forest floor by Red Squirrels in our plots between the 2 sampling periods, we estimated that the 9.3 kg of dry litterfall would provide forage for 0.226 deer/d/ha during the winter. We corrected for moisture content (150% of oven-dried weight) according to procedures outlined by Agee and others (2002) for Douglasfir. This estimate is based on equations developed by Waterhouse and others (1991) for a 95 kg adult female Mule Deer that consumes 1.9 kg of oven-dried Douglas-fir/d.

All except 15 of the approximately 300 clippings that we scattered on the forest floor at the shelter were consumed by ungulates. Approximately 50% of the clippings were consumed by 1 elk, 20% of the clippings were consumed by 2 moose and the remaining 30% were eaten by 3 Mule Deer.

Our results suggest that Red Squirrels in winter contribute Douglas-fir twigs to the forest floor. Making corrections for the water content of clippings we collected and using established equations, we conservatively estimate that squirrels contributed forage for a minimum of

TABLE 1. Morphometric relationships between Douglas-fir twig basal diameter, width, length, and mass of 803 squirrel clippings collected from the forest floor in the John Prince Research Forest, British Columbia, February 2004.

| Х | у | r ² | r | Р | Equation |
|----------|--------|----------------|-------|-------|----------------------|
| Diameter | Length | 0.549 | 0.741 | 0.000 | y = -2.972 + 60.648x |
| Diameter | Width | 0.465 | 0.682 | 0.000 | y = -2.363 + 36.815x |
| Diameter | Mass | 0.577 | 0.760 | 0.000 | y = -7.089 + 42.308x |
| Width | Mass | 0.488 | 0.698 | 0.000 | y = -1.703 + 0.720x |
| Width | Length | 0.535 | 0.732 | 0.000 | y = 4.274 + 1.109x |
| Length | Mass | 0.542 | 0.736 | 0.000 | y = -2.817 + 0.501 |

0.226 deer/d/ha. Given that there are approximately 14,000 ha of Mule Deer winter range available in our study area, our calculations suggest that Red Squirrels (if equally distributed throughout the winter range) could provide a minimum of 3200 deer-days of Douglas-fir forage during late winter. Again, our estimates are conservative because they do not account for clippings that we were unable to locate because they had already been consumed by Mule Deer or other species on our plots. Given that Douglas-fir boughs comprise half of the Mule Deer winter diet in the study area (Hodder 2009), it appears that Red Squirrels could contribute a substantial portion of the winter diet of local Mule Deer populations.

Biomass inputs of Douglas-fir branches to the ground that are driven by heavy snowfall and wind events can be significant and, combined with squirrel-induced litterfall, may provide large amounts of forage for Mule Deer. Hoffman (1985) classified Mule Deer as concentrate feeders due to a relatively smaller rumen and reticulum than larger bulk feeding ruminants, such as Moose. As central place foragers, Red Squirrels (Elliott 1988, Gurnell 1984) can provide relatively large amounts of potential forage for Mule Deer in centrally located areas in forest stands with high canopy closure. Thus, Mule Deer can access high quality forage when mobility in other areas may be restricted due to deep snow conditions. The snow interception provided by old growth Douglas-fir combined with preferred forage opportunities create optimal winter conditions for Mule Deer.

Plants within reach of animals are slowly stripped of their most nutritious parts over the winter months by the host of herbivores that depend upon them (Windels and Jordan 2008). For this reason, biomass contributed to the forest floor by Red Squirrels could serve a potential and critically important food source to selective foragers such as Mule Deer that find it difficult to locate forage in winter (Blood 2000; Mackie and others 2003).

Although we have noted that it is common to find Mule Deer tracks among Red Squirrel clipped twigs, we have not directly observed the use of squirrel clippings by Mule Deer in a natural setting. However, Edelman and others (2005) reported photographing White-tailed Deer (*Odocoileus virginianus*) in occupied Red Squirrel middens, albeit no evidence of White-tailed Deer eating from Red Squirrel caches was reported. Dawson and others (1990) noted that Mule Deer do eat the top boughs of large conifers clipped and left on the ground by humans during cafeteria-style feeding trials. Additionally, we have noted during our feeding experiment that twig clippings of the dimensions contributed to the ground by squirrels are eaten by humanhabituated Mule Deer, as well as Moose and Elk. Deer did not eat as many twigs as the Moose and Elk, but it was difficult to ascertain whether or not this was due to the attractiveness of the forage or the interspecific interactions between the animals and some of the antagonist behaviors of the Moose and Elk towards the deer and one another while feeding. These observations together suggest that Douglas-fir clippings provided by Red Squirrels are very likely to serve as a winter food source for Mule Deer in some areas.

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