

The Influence of Willow *Salix* sp. Rose Insect Galls on Moose *Alces alces* Winter Browsing

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Feeding trials were conducted with Moose (*Alces alces*) habituated to people to determine whether Moose prefer winter shoots of Scouler's Willow (*Salix scouleriana*) with or without leafy willow rose insect galls created by rosette willow gall midges (*Rabdophaga* spp.). After sampling one or two shoots with galls, each Moose in the feeding trial showed a clear aversion to the galls and dropped or spit out parts of the willow shoot containing these structures in subsequent feeding bouts. Despite the reported importance of leafy materials in the fall and winter diets of Moose, these results suggest that morphological attributes of or chemical deterrents within galls may lead Moose to reject these structures in favour of gall-free shoots. Why galls are rejected is speculated upon, but remains untested.

Key Words: Moose, *Alces alces*, browse, feeding trial, gall, rosette gall, shoots, Scouler's Willow, *Salix scouleriana*, willow rose, *Rabdophaga* sp., Cecidomyiidae.

Moose are generalist herbivores and forage on a variety of seasonally available materials such as grasses, forbs, aquatic plants, lichens, and twigs of various shrubs and trees (Renecker and Schwartz 1998). In winter, Moose subsist predominantly on woody twigs and bark (Renecker and Schwartz 1998), but they are also known to consume leafy needles of coniferous plants (e.g., *Abies lasiocarpa*, Subalpine Fir, and *Pseudotsuga menziesii*, Douglas-fir) (Bergerud and Manuel 1968). Moose even select for and consume senescent and fallen leaves rather than twigs in winter as long as leaves are accessible (Renecker and Hudson 1985). Why Moose prefer autumn leaves to shoot materials is unknown, but it is likely related to leaves generally being more digestible (containing less fiber) than twigs (Renecker and Hudson 1988).

Several midge species of the genus *Rabdophaga* (Diptera: Cecidomyiidae) form stem or shoot tip galls on numerous species of willows (*Salix* spp.) (Darlington 1975; Samsone et al. 2011) that are eaten by Moose (personal observations). Unlike nodular galls, however, galls induced on the vegetative buds of willows by ovipositing insects, such as the European rosette willow gall midge (*Rabdophaga strobiloides* (occas. as *rosaria*)), form neoplastic structures called terminal rosette galls or willow roses (Darlington 1975; Samsone et al. 2011). These galls are composed of 30 to 60 leaves

shortened and crowded together on affected shoot tips (Stubbs 1986; Samsone et al. 2011). In most cases, the formation of the gall inhibits shoot elongation as resources from the shoot become incorporated into the gall (Nyman et al. 2011; Samsone et al. 2011).

Rosette galls begin to form with leaf expansion in early summer and provide shelter and nutrition around the developing midge larvae, which typically pupate within the gall (Nyman et al. 2011). When fully developed in late summer, galls appear red to green in colour and similar in shape to the solitary inflorescence of an ornamental rose (*Rosa* spp.), hence the name. Rosette galls turn brown in autumn and can persist in substantial numbers on willows over winter. As such, these structures represent a potential pool of accessible leafy materials for Moose and other herbivores to eat at a time of the year when leaves and other herbaceous resources are scarce.

Studies indicate that shoots with galls are highly attractive to some herbivorous insects (Nakamura et al. 2003) and that galling insects are found more commonly on the shoots of trees previously browsed by moose (Danell and Huss-Danell 1985); this has not been tested in British Columbia. Because Moose often select the shoots of previously browsed rather than unbrowsed plants (Danell et al. 1985), it follows that Moose will be faced with the choice of consuming or avoiding galls



FIGURE 1. Photograph of a typical stem of Scouler's Willow (*Salix scouleriana*) with associated shoots (one with and one without a rosette gall) collected near Bednesti Lake for the feeding trial.

while feeding. However, this could depend in large part on both the morphological and chemical attributes of galls (Roininen et al. 1997).

Here, I tested whether, given a choice, Moose prefer shoots with willow roses or without willow roses (I assumed that willow roses constituted leafy material as defined by Renecker and Hudson (1985)) induced by *Rabdophaga* sp. near *salicisrhodoides* (Osten Sacken). My hypothesis was that, when offered plants with willow roses during winter, Moose would select shoots with willow roses rather than shoots without.

Methods

Shoot collections

On 16 February 2007, I collected shoots with and without willow roses from 28 Scouler's Willow (*Salix scouleriana*) plants which are commonly browsed by moose in northern BC in winter (Rea and Gillingham 2001). All collections were taken from plants growing along the verge of the Bednesti Lake South Road, Bednesti Lake, British Columbia (53°50'54"N, 123°21'32"W), 50 km west of Prince George. Stem collections were made at between 0°C and 4°C. From each plant, I harvested between 1 and 10 stems containing willow roses, for a total of 79 stems. I collected only stems that contained a shoot with a gall and a shoot

of similar length and basal diameter originating from the same stem without a gall; shorter or longer shoots on the same stem were removed (Figure 1). In this way, each stem that was presented to a Moose provided a choice of two shoots—one with a gall and one without a gall.

A small mark was placed at the base of each shoot that contained a gall so that each shoot containing a gall could be identified after the feeding trials. Stems were packaged in plastic bags and transported in an unheated car roof rack carrier at ambient outdoor temperatures (−10°C to 7°C) to the feeding site.

Feeding trials

Feeding trials were conducted at the Northern Lights Wildlife Shelter run by the Northern Lights Wildlife Society in Smithers, B.C. (54°50'N, 127°04'W), approximately 4 hours west of the collection site by car. On 17 February 2007, stems containing shoots with and without willow roses were presented one at a time by six students from the University of Northern British Columbia to five Moose habituated to people. The Moose ranged in age from 9 to 33 months (Figure 2).

Moose were allowed to smell and test the stems before biting them. Once a bite was made, the stem was retracted from the reach of the Moose momentarily so



FIGURE 2. When Moose browsed shoots, they mouthed the shoot until they appeared to find the desired bite diameter, then they cropped the shoot from the stem. Shoots were then manipulated in their mouths until the tips were either consumed (tips without willow rose galls) or dropped (tips with willow rose galls).

that a determination could be made as to which shoot (the one with the gall or the one without the gall) had been selected first and at what diameter the shoot had been browsed. Stems were bagged following the offering and another set of shoots was presented to the Moose. The feeding trial took approximately 60 minutes.

Analysis

Analysis of variance (ANOVA) was used to test differences in attributes of shoots with and without willow roses, both before and after browsing by Moose. I used a Z-test to test the statistical significance in the order of consumption by Moose of galled and ungalled shoots (Zar 1984).

Results

The formation of galls on shoot tips presumably truncated the lengthwise extension of the shoots during summer growth. Selecting shoots of similar morphology (i.e., basal shoot diameter and taper) for the experiment therefore resulted in the shoots that contained galls being significantly shorter than those without galls (ANOVA) (Table 1). Despite these initial differences in shoot length, Moose cropped shoots at similar diameters, leaving similar post-bite shoot lengths (Table 1). With the exception of three shoots that contained galls and seven shoots with normal tips, Moose cropped both shoots on all stem pairs (the shoot with and the shoot without a willow rose) presented in the feeding trials.

TABLE 1. Differences in the mean physical characteristics (with standard error) of gall-bearing and non-gall-bearing shoots of Scouler’s Willow (*Salix scouleriana*) before and after being bitten by Moose (*Alces alces*). Note: Shoot tip first bitten does not equal 100% because some shoots remained unbitten, or both shoots in a pair were bitten at the same time.

Characteristics	Shoot tip type				P of ANOVA
	with willow rose galls		without willow rose galls		
	%	Mean	%	Mean	
Pre-Bite shoot length (mm)	–	31.49 ± 1.55	–	44.99 ± 1.54	<0.001
Post-Bite length (mm)	–	14.82 ± 1.26	–	15.32 ± 1.40	0.889
Bite diameter (mm)	–	3.79 ± 0.11	–	3.66 ± 0.12	0.796
Shoot tip first bitten	51.6	–	41.8	–	–

Twigs containing willow roses were selected first by Moose 51.6% of the time, and twigs without willow roses were selected first 41.8% of the time; the remainder remained unbitten or were bitten simultaneously (Table 1). Of the 79 stems that contained galls with which we experimented, 60 galls were not consumed by Moose and were recovered from the ground after the feeding trial. One or two galls appeared to have been sampled by each Moose, but most galls were rejected and dropped to the ground. Moose consumed significantly more ($\hat{p} = 0.434$, $Z = -8.738$, $P \leq 0.001$) of the shoots with normal tips, with only 2 partial tips of the normal shoots being located on the ground after the feeding trials (compared to 60 shoot tips with galls). All shoot materials were easily detected atop the compacted, snow-covered feeding grounds. The average bite diameter on the shoot attached to the underside of the willow rose where the Moose had cropped off and spit out the willow rose while chewing the shoot, was 3.26 mm (SD 1.18). The average diameter of willow roses (measured at the widest part of the rose) was 34.106 mm (SD 11.054).

Discussion

Browsing by Moose and Reindeer (*Rangifer tarandus*) is known to affect the activity of galling insects (Danell and Huss-Danell 1985; Olofsson and Stregbom 2000; den Herder et al. 2004). Insect activity is generally greater on those plants that have previously been browsed by Moose (Roininen et al. 1997). Galling aphids respond similarly to browsing of some plant species by cattle (Martinez and Wool 2003). However, the way in which gall-forming insects influence Moose browsing directly through gall formation on browse plants appears, until now, to have gone unreported. Here, Moose clearly selected against shoots that contained galls during winter—a finding counter to my original hypothesis of Moose in winter seeking out larger, leafier bites while browsing.

My pre-feeding data indicate that winter shoots containing willow roses are shorter on average than those shoots without galls. This was expected and is an artifact of gall formation (Nyman et al. 2011; Samsone et al. 2011) which allows the shoot to continue to develop in girth and taper (those characters I sought to enable by pairing shoots on main stems), but not in length. Despite these initial differences, Moose cropped both types of shoots so that the remaining lengths of shoots and the associated bite diameters showed no significant differences between shoots with and without galls. This was accomplished by Moose cropping each bite well below the shoot tip at an average diameter of 3.7 mm, removing the shoot from the stem, and then consuming the shoot from the more proximal to the more distal portion of the shoot through oral manipulation. Upon reaching the end of the shoot, Moose would consume

(in the case of the ungalled tips) or spit out (in the case of shoots that contained galls) the shoot tip.

Unlike Iberian Wild Goats (*Capra pyrenaica*) of Spain's high Sierra Mountains that eat flower buds of the high Mediterranean shrub *Hormathophylla spinosa* with or without spheroid chalcid wasp galls (Zamora and J. M. Gómez 1993), Moose showed a clear and unexpected preference for willow shoots that did not contain rosette galls. During the trial, it appeared as if each Moose sampled one or two galls before systematically rejecting them in subsequent feeding bouts. This outcome suggests that leaves of willow roses are likely of a different quality than fallen leaves, which Renecker and Hudson (1985) reported comprised an important part of the early winter diet of Moose.

The differences in palatability of willow roses on the one hand and fall and winter leaves and leaf litter on the other, may be attributable to the differences in the morphology of normal willow leaves and willow roses. Chemical differences in shoots with and without galls may also explain differences in palatability. Galls produced by some insects contain 10 times the amount of tannins found in surrounding or gall-free tissues (Cornell 1983). An increase in oxidative enzyme activity was recently found to be present in rosette gall tissues, leading Samsone et al. (2011) to suggest such increases offer protection to larvae within the gall against generalist herbivores. The chemical constituents, if any, that may have led Moose to reject galls, however, remain undetermined.

In the years since the feeding trials, I have noticed freshly cropped willow roses on top of the snow twice in areas where Moose had been recently feeding, again suggesting that Moose have some aversion to these galls. Clearly, further research into whether rejection of such tissues by Moose is based on morphological or chemical characteristics of willow roses is required and may eventually help to explain that, for Moose, bigger mouthfuls are not always necessarily better.

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