

**The effect of an introduced predator scent on mule deer
(*Odocoileus hemionus*) browsing activities in meadow
habitats in Gothic, Colorado**

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Abstract. Scientists in the Rocky Mountain Biological Laboratory (RMBL) have observed an increase in mule deer (*Odocoileus hemionus*) populations within the Gothic town site, as well as an increment in plant browsing. Our research group hypothesized that mule deer have become more common in Gothic during the summer because they avoid coyotes (*Canis latrans*), who avoid the town site. This could represent a trophic cascade (i.e., a cascade of effects among species across trophic levels) which ultimately influences browsing of plants. We first wanted to know if deer are more common in Gothic than outside the town. To explore this I used observations in and out of town. Second, we wanted to know if herbivory is greater in town. To explore this I recorded browsing of plants along transects in and out of town. Third, we hoped to mimic coyotes by putting out coyote urine in some meadows in Gothic, pairing these meadows with controls lacking urine. I recorded deer browsing in meadows with and without urine. Results indicated that deer are more common in town than out of town, but browsing rate was not significantly different in the two places, although the trend was in the expected direction. I also found no clear effect of coyote urine on plant browsing, and no evidence that urine repels deer. Higher density of deer in Gothic might be due to absence of coyotes, but we cannot exclude other possibilities. We have learned a lot, but more study of this will be welcome.

Keywords. mule deer, *Odocoileus hemionus*, plant herbivory, trophic cascades

Introduction

Over the years, the study of trophic cascades has evolved from a minor part of ecology to a major endeavor that considers multiple and dynamic interactions within nature. The term trophic cascade concerns the interactions between primary producers and higher levels of consumers, and how those interactions can alter the abundance and productivity of populations of a specific trophic level (Pace et al. 1999). Current research in this field aims to understand trophic cascades as important considerations for ecosystem management, restoration, and conservation policies (Pace et al. 1999). Within terrestrial ecosystems, trophic cascades appear to be common (Pace et al. 1999, Schmitz et al. 2000). In these systems, predators can have indirect and direct effects on prey community structure and dynamics (Schmitz 2000, 2004, Hebblewhite et al. 2005, Beschta

and Ripley, 2009), their behavioral activities, their habitat selection (Schmitz 2000, Hebblewhite et al. 2005), and ultimately on the plants (Schmitz 2000, Schmitz et al. 2004).

Previous research has shown that human activities can also shift and mediate trophic cascades (Hebblewhite et al. 2005). Because large predators tend to avoid places with heavy human activity, human presence in a particular system can play an important role in lowering predator densities and in changing their spatial distribution. Predator population shifts can lead to a reciprocal shift in density of prey, since prey may be inclined to gather in areas with few predators and lower predation risk. An example of this is a study with wolves (*Canis lupus*) at Banff National Park in Canada, in which human activity was found to strongly influence the use of space by wolves and thus their predation (Hebblewhite et al. 2005). Moving to the next-lower trophic level, reduced predation and therefore more herbivores in a system might lead to excessive browsing of plant communities.

Herbivory generally has negative effects on plants fitness (Shelton and Inouye 1995, Knight 2003). As browsing herbivores, deer tend to feed preferentially on some plants and avoid others; therefore, they have the capacity to alter the structure and composition of plant communities (Rooney and Waller 2003). Herbs may be more vulnerable to deer browsing than woody plants because they never grow sufficiently to escape browsing impacts (Rooney and Waller 2003). Most of the literature about deer herbivory impacts on woody plants and forbs has concentrated on white tailed deer (Waller and Alverson 1997, Fletcher et al. 2001, Coomes et al. 2003, Horsley et al. 2003, Knight 2003, Rooney and Waller 2003, Cote et al. 2004, McGraw and Furedi 2005, Farrington et al. 2009), and much less is known about mule deer herbivory, especially in the Western USA. Thus, there is a lack of scientific knowledge on browsing of

forbs by mule deer in Colorado, and closing this gap in knowledge is crucial for management efforts aimed at preserving communities of native and abundant wildflowers in the state.

Over the last couple of decades, scientists in the Rocky Mountain Biological Laboratory have noticed (but not measured) an increase in mule deer (*Odocoileus hemionus*) populations within the Gothic townsite. They also have noticed (but not measured) an increment in plant browsing. These observations led to the idea that mule deer have become more common within the field station during the summer because one of their natural predators, the coyote (*Canis latrans*), avoids the townsite. In fact, the larger question is whether there is a trophic cascade between humans, coyotes, deer, and plants. This cascade was hinted at by the study of Reneé Arozqueta (RMBL REU 2005). She explored deer abundance and intensity of browsing on herbaceous plants and gained some evidence that deer have become more common in Gothic .

This paper is part of a team effort to continue the study of the human-coyote-deer-plant (“HCDP cascade”). I proposed to address three research questions: (1) Are deer more common in the Gothic townsite or out of town?; (2) Are plants more heavily browsed by deer in town or out of town?; (3) Are plants more heavily browsed by deer in meadow areas scented with coyote urine than in a control meadows?

Methods

Study Site

I worked at the Rocky Mountain Biological Laboratory (RMBL), an independent field station located in Gothic (CO) at ca. 2900m elevation in the East River valley of the West Elk mountains of Colorado, USA (Inouye et al. 2000).

Deer Scan Observations

To address question (1)—are deer more common in the Gothic townsite or out of town—I conducted deer scanning observations in three vantage points, one located within town (Gothic point; see Figure 1) and two located outside (North Gothic point and South Gothic point; see Figure 1). At each vantage point, I sat still for about an hour and a half, and every ten minutes I scanned with a pair of binoculars all my visual area (drawn in the map as color coded polygons; see Figure 1) and recorded the number of deer I saw (distinguishing between fawns, does, and bucks), their behavior (foraging, walking, running, standing, lying down or playing) and their estimated location (with the help of GIS aerial photographs used as maps). Deer scanning observations were conducted three times a week, once per site, at dawn and dusk. Our weeks of deer observations were divided into blocks, one block per week to facilitate the analysis, and with this we wanted to obtain an equal sampling effort at each site during each time period, to avoid having temporal changes in deer activity affect our estimates of in vs. out of town activity.

Deer scans were averaged per date of observation and per site of observation. I calculated the number of deer per instance as follows: $\text{total deer sighted in a period of observation} / \text{total number of scans} \times \text{total hectares of scanned area}$. The statistical analysis used to interpret these data was an ANOVA.

Vegetation sampling – Plant herbivory transects out of town

To address question (2)—do deer browse more in town or out of town—I conducted plant herbivory transects out of town in the sites where my deer vantage points were located (North Gothic and South Gothic). The areas chosen for transects were selected in a random manner, but guided by the interpretations of my deer scanning observations. For each site, I established two nine meter transects, in localities where deer were observed to be common and where the

vegetation appeared to be similar in composition to our sites in town. On each transect I and my assistants counted and identified any herb individual that directly intersected the transect string and was taller than five centimeters. Additional herb individuals were also counted and identified if one of their stems or leaves touched the transect string, even if their stem did not, and if they were within 20 cm from the string. We tried to include only stems that we thought were part of the same plant, but this was very difficult since we could not dig up plants. To measure browsing I counted the numbers of browsed and total shoots or flowering stems on each plant. Data collected from transects out of town and in the townsite were compared with ANOVA.

Introduction of a predator scent

Previous studies have showed that predator odors can have an effect on its prey behaviors, and can also suppress feeding activities (Sullivan et al. 1985, Apfelbach et al. 2005). In a previous RMBL-REU study, Trixie Lee (RMBL REU 2005) found mule deer that exposed to coyote urine increased their vigilance state and use the urine scent as a predation risk cue. I hoped to use coyote urine to answer question (3)—Are plants more heavily browsed in areas scented with coyote urine than in a control meadows—and thereby to test the idea of the “HCDP” trophic cascade. My collaborators and I selected three study sites within the Gothic townsite: Johnson meadow, the Research meadow and the South Gothic meadow (see Figure 1). Each study site had two treatments stations (urine scent and control) that were separated by approximately 120 m. The control and scent treatments were assigned at each site by flipping a coin, setting them up as randomized blocks. Each station consisted of four Petri dishes placed in a squared orientation on the soil, and each Petri dish had 10 mL of a polyacrylamide gel called Terrasorb (Garden Harvest Supply Inc., Indiana, USA), plus 15 mL of the characteristic solution

for that station. For the scented treatment, the solution was coyote urine (Lexington Outdoor Solutions Inc., Maine, USA) and for the control station water. The treatment stations were monitored weekly and new solution was added twice a week.

Vegetation Sampling – Plant herbivory transects in town

On each of the three study sites, I established one or two 10 meter transects per treatment station, oriented in either North, South, East or West directions from the center of the treatment station. For each transect, I laid out a string marked in intervals of one meter. Transect observations began at one meter. Therefore each transect was 9 meters long, exactly like the transects described above that were done out of town and in the townsite. All the other details were the same as with those transects. I and my assistants censused these transects two times, one at the beginning of the flowering season in June and one towards the end of my field work in mid July. I analyzed the data with an ANOVA.

Vegetation Sampling – Focal plant herbivory observations

According to the previous study by Arozqueta (2005) and other anecdotal evidence from RMBL researchers, the plants most commonly browsed by deer in meadow habitats within Gothic are *Helianthella quinquenervis* (aspen sunflower), *Valeriana occidentalis* (western valerian), *Ipomopsis aggregata* (scarlet gilia), *Valeriana edulis* (edible valerian), *Aquilegia coerulea* (blue columbine, Colorado's state flower) and *Ligusticum porteri*. To complement this previous work and to complement the focal plant studies described above—in answer to question (3)—I flagged up to ten focal plants for each of these preferred species at each treatment station in each of the three study sites, and measured weekly the number of flower stalks browsed by deer and the total number of flowering stalks. All focal plants were randomly selected and were

within a 10 meter by 10 meter plot centered on the treatment station. We analyzed data collected for the following “focal” species: *Ipomopsis aggregata*, *Ligusticum porteri*, *Valeriana edulis* and *Valeriana occidentalis* (see Figures 6 to 9). We calculated the change each week in browsing =for each focal species (see Table 4) using the equation rate of change = $\Delta \text{Cumulative Proportion Browsed} / \Delta \text{Time (in weeks)}$. The analysis applied to these data (Table 4) was a Paired t-Test.

Results

Deer scan observations

During six weeks of observation I saw a distinct difference in abundance of deer spotted in each site throughout time (F ratio = 3.6004, df = 5, p = 0.0265; see Figure 2). Deer sightings increased exponentially through time until the fourth week, decreased in the fifth week, and then increased again in the sixth week. This suggests that deer may have different activity peaks during the summer season. There was no significant difference in numbers of deer sightings between early morning (dawn) and late afternoon (dusk) observation periods throughout the entire period of observations (F ratio = 0.0055, df = 1, p = 0.9422). This discovery allows us to pool all of our deer observations, regardless of the time of day, for subsequent analysis. There was a clear difference in abundance of deer at our different sites (F ratio = 21.7017, df = 2, 30, p < 0.0001; see Figure 3), showing that deer frequented the Gothic townsite (mean = 0.0991, std. error = 0.0165) followed by the South Gothic site (mean = 0.0099, std. error = 0.0181), and did not visit the North Gothic site at all (mean = 0.0000, std. error = 0.0173). A significant block by site interaction demonstrated that there was also a significant difference among each of our sites throughout our whole observation period (F ratio = 3.1793, df = 10, p = 0.0240), meaning that variation in deer activity densities differed from site to site. Finally, to determine if deer were more common in town than out of town, we did an orthogonal contrast between the Gothic site and the South and North Gothic sites

(F ratio = 40.5958, df = 1, 30, $p < 0.0001$), which turned out to be highly significant, therefore deer activity is higher in the Gothic town site than out of town (see Figure 3). This analysis was supported by calculating the number of deer per instance (= total deer sighted in a period of observation / total number of scans $\times$ total hectares of scanned area), for which we found that deer are more active in town ($G = 0.095$ deer/scan*ha; see Table 1) than out of town ($SG = 0.006$ deer/scan*ha, $NG = 0.000$ deer/scan*ha; see Table 1). In addition, we conducted a second orthogonal contrast between the North Gothic and South Gothic sites (both out of town sites) and found that these sites were not significantly different one from one another (F ratio = 2.2254, df = 1, 30, $p = 0.1462$). Hence deer do not seem to have a preference to spent more time in the South Gothic site over the North Gothic site; although deer activity records suggest that they do (see Figure 3).

Plant transects studies – in vs out

Besides sightings of deer, plant transects in town and out of town could help us discern where browsing activities were higher. Analysis done with all of our plant transect data, using residuals from overall mean browsing proportion for each species, suggested that there was not a significant site effect (F ratio = 1.3240, df = 2, 308, $p = 0.2676$; see Figure 4.A), therefore we could not conclude that deer browse more in town vs. out of town. A repeated analysis only using the preferred plants encounter along the transects (those that were actually browsed) also revealed no site effect (F ratio = 1.4443, df = 2, 208, $p = 0.2383$; see Figure 4.B), although trends of mean residuals from overall browsing proportion for each species suggested each site had different browsing patterns.

Plant transect studies – experimental sites in town

To examine if deer foraging activities in town changed with the introduction of coyote urine scent treatment, plant transects were conducted on both scented and control treatments in our three study sites. Using the Expected Mean Squared (EMS) Method in an ANOVA with the residual proportion of browsed shoots per plant, we found that the two censuses conducted during the summer did not differ (F ratio = 3.5049, df = 1, p = 0.0616), although plants in the second census (mean = 0.0117, std.error = 0.0117) seemed to be more browsed than in the first census (mean = -0.0045, std.error = 0.0071). Additional evaluation revealed that there was no significant site effect (F ratio = 1.1342, df = 2, p = 0.4685), although data suggested that Johnson meadow (mean = 0.0307, std.error = 0.0320) was more heavily browsed than South Gothic meadow (mean = -0.0203, std.error = 0.0429) and Research meadow (mean = -0.0265, std.error = 0.0341). There was no significant difference between the coyote urine and control treatments (F ratio = 0.6372, df = 1, p = 0.5078). Deer actually appeared to be eating more in the scented treatment overall (mean = 0.0181, std.error = 0.0290) than in the control treatment (mean = -0.0198, std.error = 0.0308). We also found a significant site by treatment interaction, which means that the treatment effect varied from one site to another (F ratio = 10.8709, df = 2, p < 0.0001), even though site and treatment alone did not matter much to deer. To summarize the sites and treatments in order from most to least browsed, JM, Scented (least sq. mean = 0.0919, std. error = 0.0136) > RM, Scented (least sq. mean = -0.0273, std. error = 0.0144) > SG, Control (least sq. mean = -0.0172, std. error = 0.0199) > RM, Control (least sq. mean = -0.0148 , std. error = 0.0144) > SG, Scented (least sq. mean = -0.0135 , std. error = 0.0164)> JM, Control (least sq. mean = -0.0118, std. error = 0.0128).

Plants preferred by deer

The plant transect data show that deer preferred some plants over others (F ratio = 4.6943, df = 48, 1162, $p < 0.0001$; see Table 2). The most highly preferred plants were *Oreochrysum parryi* (mean = 1.0000, std. error = 0.1443), *Tragopogon pratensis* (mean = 0.8750, std. error = 0.1020), *Aquilegia coerulea* (mean = 0.2111, std. error = 0.0589) and *Helianthella quinquenervis* (mean = 0.1961, std. error = 0.0223). The least preferred plants were *Potentilla pulcherrima* (mean = 0.0245, std. error = 0.0070), *Dugaldia hoopesii* (mean = 0.0228, std. error = 0.0169), *Thalictrum fendleri* (mean = 0.0133, std. error = 0.0289), *Erigeron speciosus* (mean = 0.0043, std. error = 0.0189). In 2005, another REU student (Renée Arozqueta), using different methods, also got a glimpse of the plants that deer prefer. The proportions of browsed common species (*Aquilegia coerulea*, *Erigeron speciosus*, *Helianthella quinquenervis*, *Ligusticum porteri*, *Potentilla pulcherrima*, *Taraxacum officinale*, *Thalictrum fendleri*, *Valeriana occidentalis*, *Viola nutalli*) in Renée's data and mine were positively correlated ($y = 0.0787 + 1.2031x$, $R^2 = 0.1331$, $p = 0.0312$).

Relation between deer activity and plant browsing

To examine the relationship between deer activity and plant browsing, we correlated mean deer activity density and mean residual proportion of browsed shoots of plants for all of our study sites. This analysis required that we pool deer scan data taken by Richard Pickens with my browsing data. The relationship is positive, but it is weak and is not significant ($y = 0.0017 + 0.2174x$, $R^2 = 0.0963$, $p = 0.4545$; see Figure 5). The only strong relationship found was in the scented treatment in Johnson Meadow (mean deer activity = 0.12170, mean residual prop.BS = 0.0825, std. error of mean residual prop. BS = 0.0544; see Table 3).

Focal plant herbivory observations

To better understand deer browsing activities in our experimental sites in town, we graphed data for the focal plants in scatter plots that related time in weeks with the cumulative proportion of browsed flower stalks for that particular species. For *Ipomopsis aggregata*, found only on Johnson meadow, the scented treatment was more browsed than the control treatment (Figure 6). *Ligusticum porteri* was not found in the same site for both treatments, but it was spotted at two different sites; *Ligusticum* results suggest that it was more browsed in the scented treatment of Johnson meadow than in the control treatment of South Gothic meadow (Figure 7). For *Valeriana edulis*, located at Research meadow, browsing effects did not seem that different, although this plant was more browsed in the scented treatment than in the control treatment (Figure 8). *Valeriana occidentalis* was our strongest comparison over the three experimental sites because it was common at the beginning of the summer in all of them. In Johnson meadow and Research meadow, *Valeriana occidentalis* was more browsed in the scented treatment than the control treatment (Figure 9.A, Figure 9.B), but in South Gothic meadow it was more browsed in the control treatment than the scented treatment (Figure 9.C). After observing the browsing trends for each focal species, we calculated the browsing change per week for each of the focal species (Table 4). A paired T-test showed that there was no significant difference in plant browsing rates among the two treatments across all of our sites ($t_s = -1.5319$, $df = 4$, $p > 0.2$ (2-tailed), $p > 0.1$ (1-tailed)), although all the focal plant browsing trends suggest that there was actually more browsing in the scented treatments.

Discussion

The purpose of this study was to assess the impacts that mule deer have on herbaceous plants by exploring how this might vary with the proximity of plants to an introduced coyote urine scent. We found that deer are more common in town than out of town, which consequentially should translate into higher plant browsing frequencies in town than out of town, but our results did not provide clear evidence of this. Within the townsite, deer activity seemed to vary throughout the summer season and among our three research sites. As found by Richard Pickens (unpublished data, 2010), deer within the town site seem behaviorally unaltered by the presence of coyote urine scent, although other studies have demonstrated that deer do react significantly to predator scent (Sullivan et al. 1985, Apfelbach et al. 2005, Lee unpublished data 2005). By examining plant browsing rates within town, I confirmed what Richard Pickens also established, that there was no scent effect on foraging. Deer actually tended to forage more in areas near scented treatments than controls, although this was not significant.

Mule deer presence in town is not completely understood, although we hypothesize that it is because they avoid coyotes. As Pickens (unpublished data, 2010) points out, coyote abundance was not successfully accounted for in and out of the town site; further work needs to be done to examine the coyote relationship with deer and plants. Another question that needs to be explored is if coyotes are the most influential predator of mule deer in Gothic; another more successful predators could be causing them to be drawn to the townsite, where there is high human activity during the summer. Another possible theory to explain why deer are more common in town is the presence of more palatable plants in the townsite. As stated by Pickens (unpublished data, 2010), within the townsite high deer activity might be related to distance to nearest cover area, as the sites with the lowest average minimum distance to cover had higher levels of deer activity.

Lee (RMBL REU 2005) also reported that deer like to stay close the forest edge. From anecdotal observations from deer scans I know that does and fawns were more commonly sighted than bucks. This information significantly relates to the fact that the study was conducted in a fawning season, which in part could explain why deer preferred to be near cover and why we observed variation in deer activity among our sites throughout the summer. In order for lactating ungulates to protect their young they must stay closer to forest or other cover (White and Berger 2001).

Plant browsing rates in and out of town did not suggest a preference for the townsite, although trends were in that direction. Plants tend to develop different strategies to account for browsing threats, such as chemical defenses that help resist s, which in part may explain why some plants are preferred over others. Anecdotal observations of our plant transects suggested that there were palatable plants that protected themselves by hiding underneath other unpalatable plants, therefore escaping browsing attempts from deer. To further assess if this impression is correct more plant transects should be conducted in and out of town. In addition, those transects should sample a broader spatial scale in order to gain a better picture of browsing rates and species composition among sites. This would help us to understand why deer are more common in some places and why they prefer some plants over others. It also would be interesting for future studies to assess the nutritional value of the plants that we think are preferred by deer.

Within the townsite, we found a difference between the two plant censuses. The first census helped us get an initial picture of browsing rates on plants at the beginning of the season, and the second better reflected the overall browsing rate of the whole season. Browsing rates varied in parallel with deer activity densities across all six sites, although they were not statistically significant; this may be due to a small sample size.

One of our most important findings was that deer foraging activities were not influenced by the introduction of a scent treatment. We did not expect this result because literature pointed to the opposite. It is known that coyotes use scent to communicate and establish territory, urine and feces being their primary markers. One of the explanations that we have for this outcome is that commercial coyote urine may be lacking a special component secreted by coyote scent glands, or it could be lost in the process of the processing of the urine. This could make commercial urine less effective than fresh coyote urine. In the future, to reevaluate scent effect on mule deer browsing activities we could replace coyote urine with fecal matter to see if this has a stronger, we could also have a smaller buffer area around the treatment to explore more small-scale effects. Differences among browsing rates in scented and control treatments could be due to proximity to forests edges as well.

Finally, our focal plant studies turned out to be one of the most efficient ways of approaching deer browsing activities because they are less time consuming to census than plant transects, and so could be sampled more times during the season. For future studies, more focal plant studies could be incorporated in more areas of the town site as well as out of town sites.

In conclusion, we can not confirm with certainty if a trophic cascade that relates humans-coyotes-deer-plants is happening at RMBL, more research needs to be conducted in order to answer this. Our methods for this research were carefully planned out, but our results suggest that they need a few modifications to improve the study.

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Tables and Figures

Table 1. Overall deer activity in and out of town.

Site	Location	N scans	mean deer/scan	σ	Area (ha)	Deer/scan*ha
G	IN	125	0.536	0.667	5.670	0.095
SG	OUT	94	0.255	0.604	43.830	0.006
NG	OUT	104	0.000	0.000	24.750	0.000

Table 2. Browse rate by plant species.

Species	Least Sq Mean prop. browsed	Mean prop browsed	Std. error of mean
<i>O. parryi</i>	1.00000	1.00000	0.14428
<i>T. pratensis</i>	0.87500	0.87500	0.10202
<i>A. coerulea</i>	0.21111	0.21111	0.05890
<i>H. quinquenervis</i>	0.19610	0.19610	0.02226
<i>Agoseris</i> sp.	0.16667	0.16667	0.05890
<i>V. edulis</i>	0.11765	0.11765	0.07214
<i>T. officinale</i>	0.10000	0.10000	0.05890
<i>C. linearis</i>	0.09524	0.09524	0.05453
<i>V. occidentalis</i>	0.08696	0.08696	0.01363
<i>V. nutalli</i>	0.05914	0.05914	0.02591
<i>G. macrophyllum</i>	0.05882	0.05882	0.02474
<i>L. porteri</i>	0.04808	0.04808	0.04002
<i>D. barbeyi</i>	0.02637	0.02637	0.04002
<i>H. parviflora</i>	0.02479	0.02479	0.04350
<i>P. pulcherrima</i>	0.02454	0.02454	0.00702
<i>D. hoopesii</i>	0.02283	0.02283	0.01689
<i>T. fendleri</i>	0.01333	0.01333	0.02886
<i>E. speciosus</i>	0.00431	0.00431	0.01895

F-ratio = 4.6943, df = 48, 1162, $p < 0.0001$

Table 3. Summary of mean residual proportion of browsed shoots (BS) of plants found in transects and mean deer activity (density) for all study sites.

Site	Treatment	Mean Residual Prop. BS (standard error of mean)	Mean Deer Activity (Density)
JM	Control	0.00920 (0.02243)	0.04480
JM	Scented	0.08252 (0.05442)	0.12170
NG	.	-0.01349 (0.01425)	0.00000
RM	Control	-0.02858 (0.00927)	0.10890
RM	Scented	0.00820 (0.02322)	0.08330
SG	Control	0.02782 (0.02747)	0.01280
SG	Scented	-0.00983 (0.02382)	0.01280
SGV	.	0.02328 (0.03189)	0.01030

Linear Regression $Y = 0.0017 + 0.217 (X)$: F-ratio = 0.6391, df = 1,6, p = 0.4545

Table 4. Paired t-test, effect of scent vs. control treatment on rate of increase in cumulative browsing for focal species. Rate is expressed as change in cumulative proportion of browsed stalks per week.

Site	Species	Scented	Control	Δ
JM	<i>I. aggregata</i>	0.0625	0.1875	-0.1250
	<i>L. porteri</i>	0.0550	.	.
RM	<i>V. occidentalis</i>	0.0362	0.0350	0.0012
	<i>V. edulis</i>	0.1680	0.1880	-0.0200
	<i>V. occidentalis</i>	0.0600	0.0575	0.0025
SG	<i>L. porteri</i>	.	0.0000	.
	<i>V. occidentalis</i>	0.0100	0.0487	-0.0387

$\Sigma\Delta = 5.0000$, mean $\Delta = -0.0360$, $s\Delta = 0.0526$, $\sigma \Delta = 0.0470$, df = 4
 $t_s = -1.5319$, $p > 0.2$ (2-tailed), $p > 0.1$ (1-tailed)

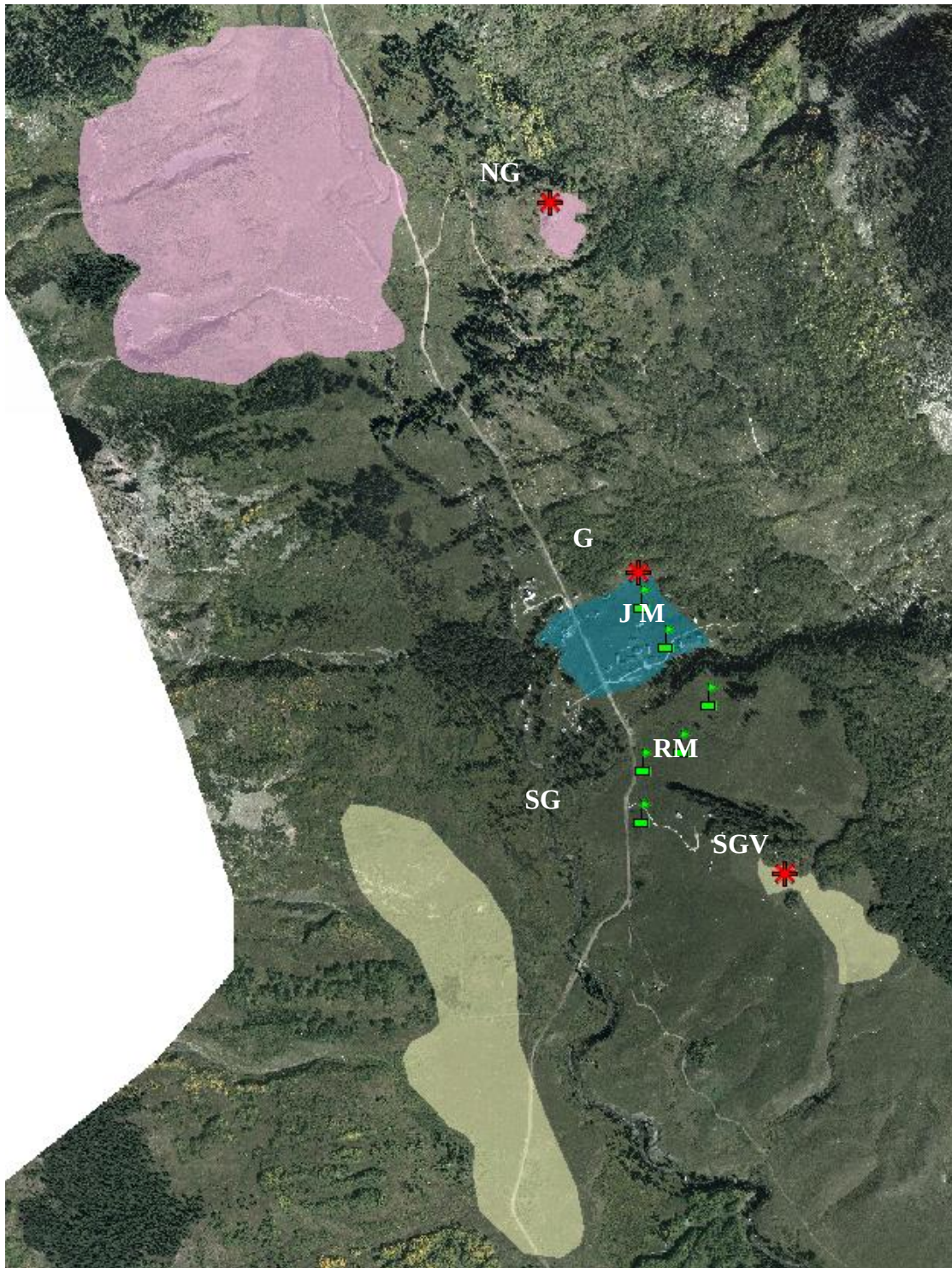


Figure 1. Aerial Map of study areas at RMBL: North Gothic (NG), Gothic (G), South Gothic (SGV), Johnson Meadow (JM), Research Meadow (RM) and South Gothic meadow (SG). Green flags show locations of experimental scented or control sites. Red asterisks show locations of vantage points from which deer scans were made; shaded polygons indicate areas visible from these vantage points (yellow=SGV, blue=G, pink=NG).

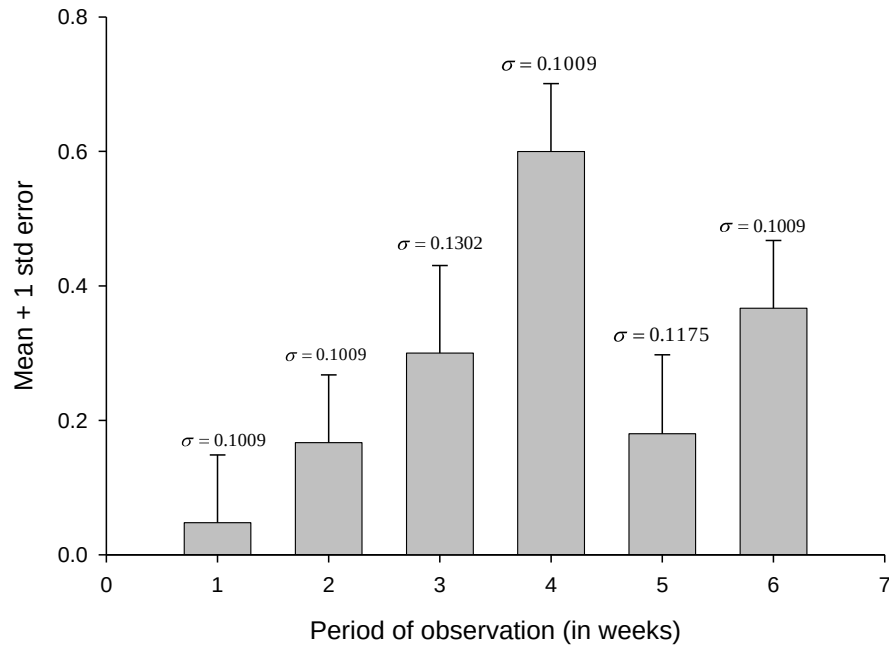


Figure 2. Mean deer observed per scan in 6 consecutive weeks of observation. Values are means + 1 standard error of the mean.

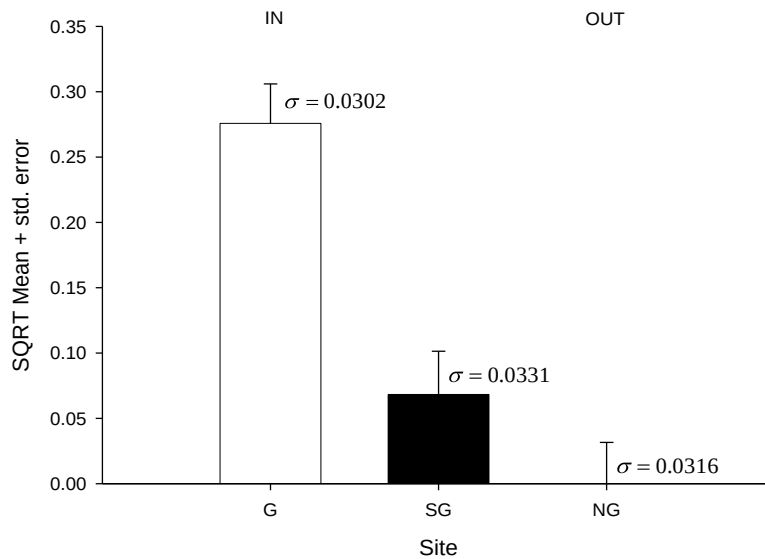


Figure 3. Deer activity (SQRT mean deer observed per scan)/(scan area) in town vs out of town. G = in town; SG and NG are out of town (values were square-root transformed for the analysis).

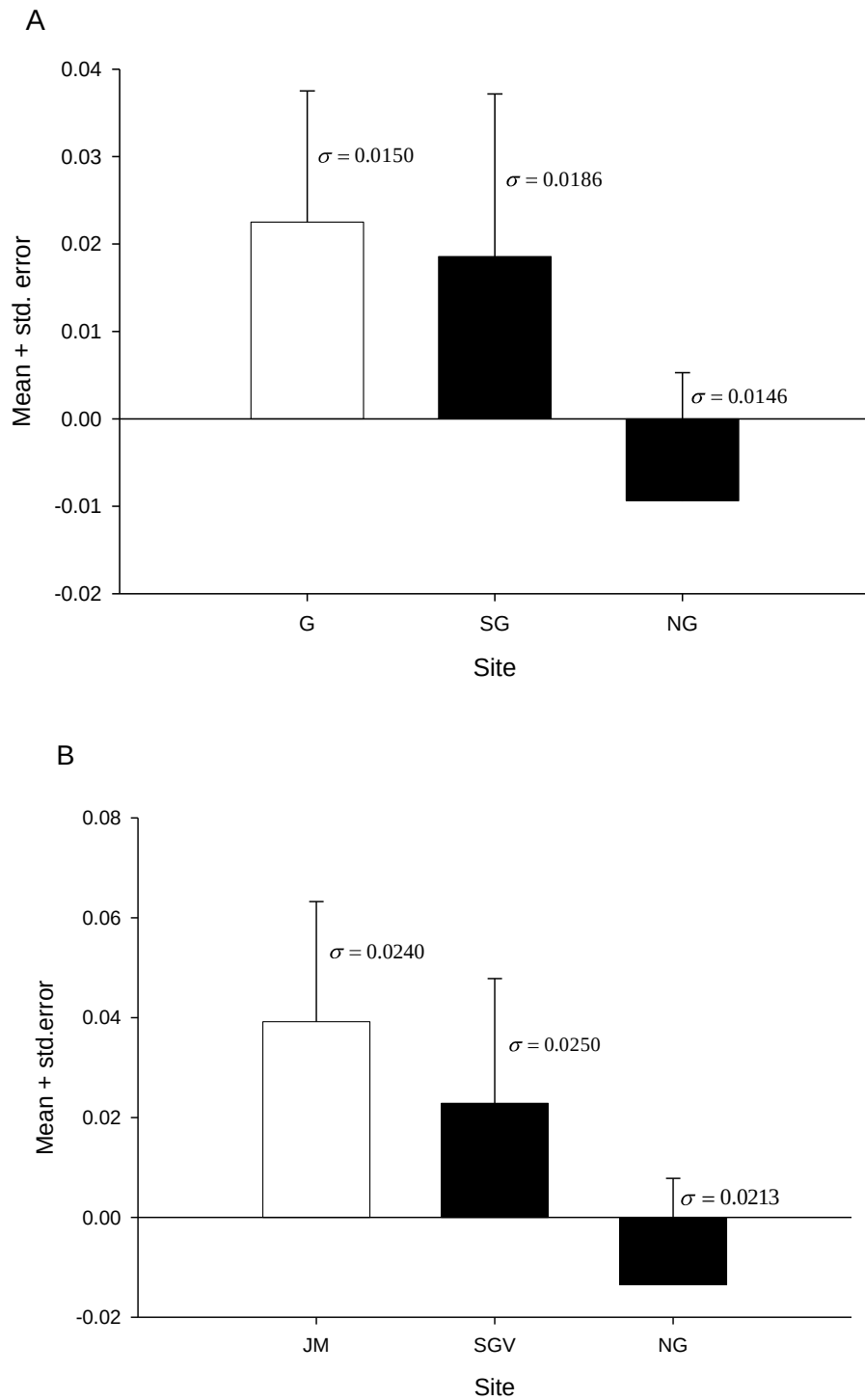


Figure 4. Effect of site on proportion of shoots browsed by deer. A) All plant species; B) Only plant species that were consumed by deer. Browsing is expressed as residual from overall mean browsing proportion for each species.

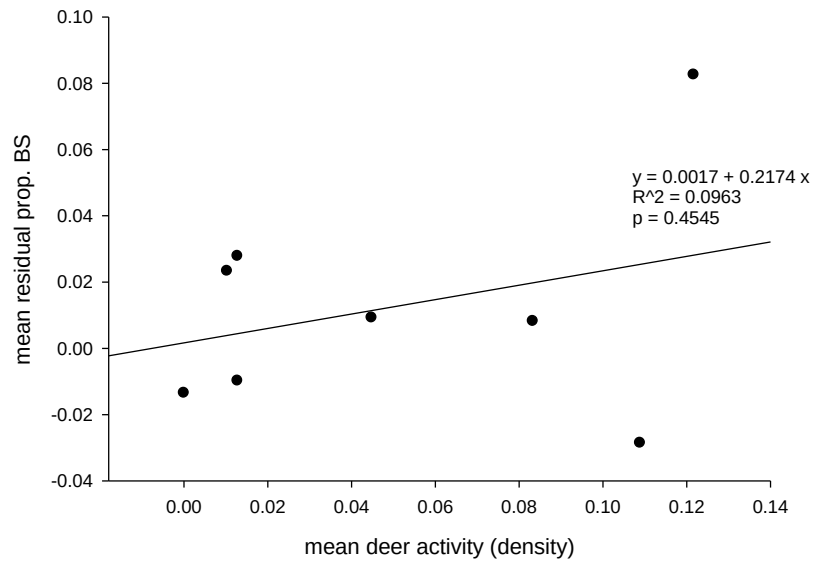


Figure 5. Relationship between deer activity density and plant browsing. Deer activity is expressed as deer observed per scan per ha; plant browsing is expressed as deviation from the mean browsing for each plant species. Values are for six sites within Gothic town site plus two sites out of town (NG, SGV).

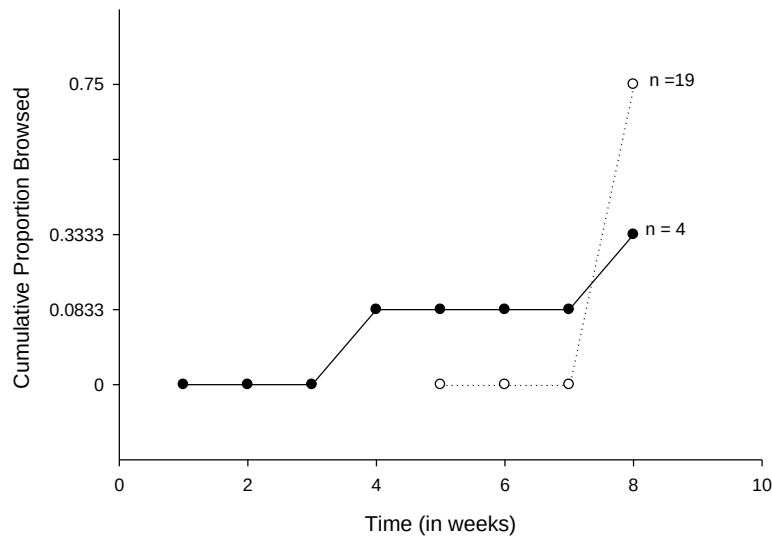


Figure 6. Cumulative proportion of flower stalks browsed for the focal individuals of *Ipomopsis aggregata* for scented (filled circles) and control (open circles) treatments at Johnson Meadow site as a function of week. The rate of increase of cumulative proportion of browsed flower stalks per week for both scented and control treatments was calculated by taking the slope of each line under the time interval from week 5 to 8.

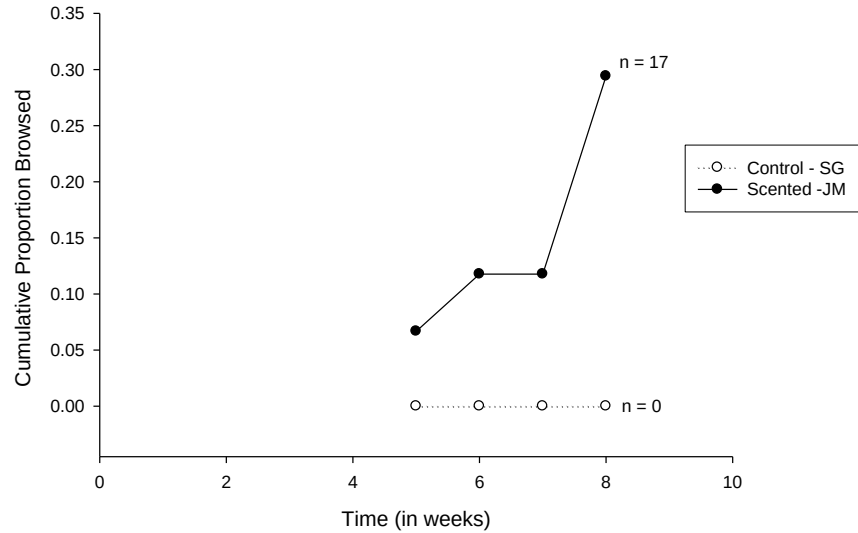


Figure 7. Cumulative proportion of flower stalks browsed for the focal individuals of *Ligusticum porteri* for scented (filled circles) and control (open circles) treatments at Johnson Meadow and South Gothic Meadow sites. The rate of increase of cumulative proportion of browsed flower stalks per week for both scented and control treatments was calculated by taking the slope of each line under the time interval from week 5 to 8.

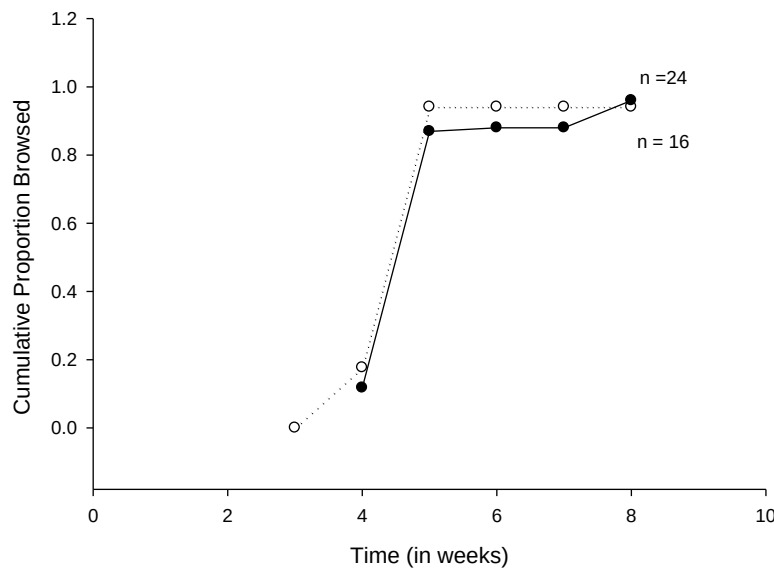


Figure 8. Cumulative proportion of flower stalks browsed for the focal individuals of *Valeriana edulis* for scented (filled circles) and control (open circles) treatments at Research Meadow site. The rate of increase of cumulative proportion of browsed flower stalks per week for both scented and control treatments was calculated by taking the slope of each line under the time interval from week 4 to 8.

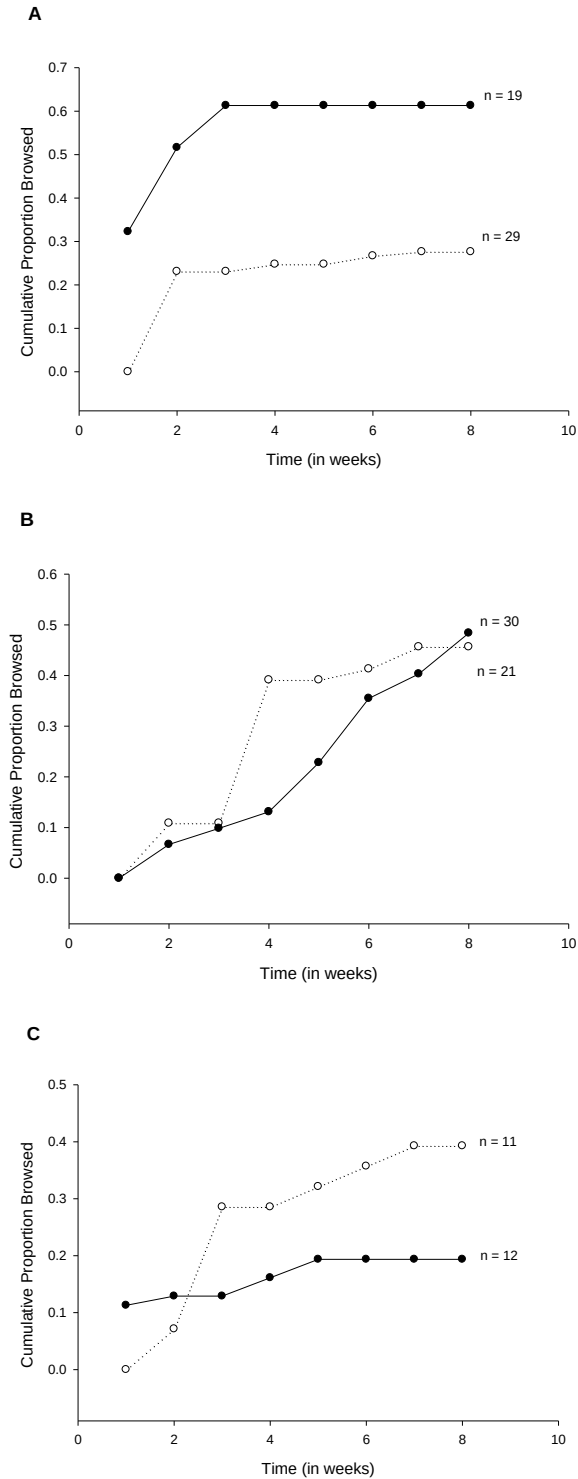


Figure 9. Cumulative proportion of flower stalks browsed for the focal individuals of *Valeriana occidentalis* for scented (filled circles) and control (open circles) treatments at Johnson Meadow (A), Research Meadow (B), and South Gothic (C) sites. The rate of increase of cumulative proportion of browsed flower stalks per week for both scented and control treatments was calculated by taking the slope of each line under the time interval from week 1 to 8.