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3 **Coyotes, deer, and wildflowers: Diverse evidence points to a trophic cascade**

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18**Abstract** Spatial gradients in human activity, coyote activity, deer activity, and deer herbivory provide an
19unusual type of evidence for a trophic cascade. Activity of coyotes, which eat newborn deer (fawns),
20decreased with proximity to a remote biological field station, indicating that these predators avoided an
21area of high human activity. In contrast, activity of pregnant female deer (does) and does with new
22fawns, and intensity of herbivory on palatable plant species, both increased with proximity to the station
23and were positively correlated with each other. The gradient in deer activity was not explained by
24availabilities of preferred habitats or plant species, because these did not vary with distance from the
25station. Does spent less time feeding when they encountered coyote urine next to a feed block, indicating
26that increased vigilance may contribute, along with avoidance of areas with coyotes, to lower herbivory
27away from the station. Judging from two palatable wildflower species whose seed crop and seedling
28recruitment were greatly reduced near the field station, the coyote-deer-wildflower trophic cascade has
29the potential to influence plant community composition. Our study illustrates the value of a case-history
30approach, in which different forms of ecological data about a single system are used to develop
31conceptual models of complex ecological phenomena. Such an iterative model-building process is a
32common, but underappreciated, way of understanding how ecological systems work.

33

34Keywords: Herbivory • plant communities • predation • Rocky Mountains • spatial distribution •
35vigilance.

36Introduction

37 Predators affect prey populations directly by killing individuals and indirectly by eliciting anti-
38predator responses such as vigilance, avoidance, and defense. These direct and indirect effects can in turn
39affect species at lower trophic levels (Pace et al. 1999). Recent evidence for such “trophic cascades”
40involving large terrestrial mammalian predators has come mostly from direct manipulations of predator
41abundance (e.g., Schmitz et al. 2000; Harrington and Conover 2007; Beschta and Ripple 2009; Ripple et
42al. 2014), which are relatively rare because of ethical, political, and financial considerations. As a result,
43we do not know how often trophic cascades occur in these systems. Other ways of detecting trophic
44cascades would be highly desirable.

45 One alternative to intentional predator manipulation is to capitalize on natural spatial gradients in
46predator abundance (e.g., Hebblewhite et al. 2005; Harrington and Conover 2007). This approach has
47allowed us to explore a possible trophic cascade in Colorado, USA, that involves coyotes (*Canis latrans*),
48mule deer (*Odocoileus hemionus*), and wildflowers. Coyotes prey on mule deer, especially young
49animals in their first year (fawns; Lingle 2000; deVos et al. 2003; Pojar and Bowden 2004), and female
50deer (does) choose to hide their newborn fawns in relatively safe habitats (Long et al. 2009). When
51coyotes are present, mule deer also tend to move from preferred feeding habitats into safer habitats, at a
52cost of lower feeding rate (Lingle 2002; see also Laundré et al. 2001). Coyotes might indirectly benefit
53plant species that deer prefer by reducing the number of deer and their feeding rates.,.

54 Fawns are born in June in the subalpine valley where we worked. Human activity in this valley is
55seasonal, peaking during summer, and is concentrated at a biological field station. Coyotes tend to avoid
56humans when possible (Gese et al. 1989; George and Crooks 2006). Based on these pieces of natural
57history, the trophic cascade hypothesis corresponds to a series of predictions about local spatial gradients
58in abundance or activity that can be compared to evidence from observations and experiments (Fig. 1).
59We made the following specific predictions. First, we predicted that coyote activity would increase with
60distance from humans, i.e., from the field station. Second, we predicted that activity of does (and their
61fawns) would be highest near the station, whereas male deer (bucks), which are not at risk from coyotes,

62 would not show a strong spatial pattern. Third, we predicted that herbivory by deer would be highest near
63 the station and positively correlated with deer activity. Here we evaluate these and related predictions
64 based on data accumulated over multiple summers of field work, and we comment more generally on the
65 value of such a cumulative process for understanding ecological phenomena.

66

67 **Methods**

68 ***Study site***

69 We worked at the Rocky Mountain Biological Laboratory (RMBL, 38.96°N, 106.99°W, 2900 m a.s.l.) in
70 the Elk Mountains of western Colorado (Fig. 2). Buildings at the station cluster within \approx 30 ha of the
71 East River Valley where the mining town of Gothic stood in the 1870s. Foot trails and unpaved roads
72 radiate from the townsite, traversing open dry subalpine meadows dominated by herbaceous perennials
73 and a few woody perennials such as sagebrush (*Artemisia tridentata*); wetter meadows supporting
74 willows (*Salix* spp.), false hellebore (*Veratrum californicum*), and other herbaceous species; open aspen
75 (*Populus tremuloides*) forest mixed with conifers; and stands of conifers, mainly Engelmann spruce
76 (*Picea engelmannii*) and subalpine fir (*Abies bifolia*), along watercourses.

77 RMBL is populated during the summer by approximately 160 humans and increasingly, over the
78 past 25 years, by mule deer—primarily pregnant does and yearling offspring early in the summer and
79 lactating does with fawns later in the summer. The deer overwinter at lower elevations and move up just
80 after spring snowmelt. RMBL policy prohibits “recreational” (non-research) feeding of animals, and food
81 or food waste is disposed of in containers that wildlife cannot open.. Thus the only food available to deer
82 (except during the behavioral experiment described below) was natural browse.

83 ***Spatial gradients in activity of coyotes and deer***

84 During timed observations of yellow-bellied marmots (*Marmota flaviventris*) in the East River
85 Valley over 9 summers, observers recorded any marmot predators seen, thus obtaining estimates of
86 diurnal coyote activity. In addition, we repeatedly walked 17–19 km of main trails during summers of
87 2010, 2011, and 2013, collected all coyote scats (feces) deposited on the trails, and mapped their

88locations. From this we calculated scat density per m of trail at different distances from the nearest
89summer-occupied cabin (Fig. 2), which estimates both diurnal and nocturnal coyote activity.

90 During summers of 2010 and 2011 we recorded activity of does, fawns, and bucks at varying
91distances from the RMBL. In 2010 we chose 6 points inside and outside of the Gothic townsite (Fig. 2)
92that afforded a clear view of a nearby meadow, and we mapped the perimeter of the “viewshed” visible
93from each point. We surveyed deer for approximately 1.5 h near dawn (0500–0700 h) and 1.5 h near
94dusk (1900–2100 h) once per week over 6 wk in June and July. During each survey period we scanned
95the viewshed every 10 min for one minute and recorded the number of deer present. . In 2011 we walked
96two standard routes inside and outside of the townsite near dawn and dusk once per wk over 6 wk in June
97and July. We scanned for deer continually as we walked each route at constant speed, and also stopped at
9824 specified points (Fig. 2) for 360° scans, each timed to last one minute. Because in 2011 the routes
99traversed habitats that differ in visibility, we mapped the perimeter of the viewshed visible from route
100segments and points by walking a life-sized cardboard image of a mule deer away from an observer
101standing on the route until half of the image was obscured by vegetation. Defining the viewshed in this
102way corrected for habitat-specific variation in visibility. We alternated the start of each route so that
103distant points were not always sampled last. Because surveys were blocked by time of day and week, we
104could sum deer counts across replicate scans and divide by scan number to arrive at a single average
105value of deer per scan for each point or route segment. Deer were sufficiently separated in space that
106double counting was not an issue. All observations in a given summer were made by the same person, to
107avoid variation arising from individual differences in visual acuity. Finally, mule deer are known to
108prefer steep topography in the presence of predators (e.g., Lingle 2002), so it is important to note that the
109survey routes did not traverse particularly rugged areas, and that ruggedness did not vary noticeably with
110distance from the townsite.

111

112

113*Behavioral response of deer to coyote urine*

114In summer 2011 we placed a feed block (Purina Mills, St. Louis, MO, USA) at each of two locations near
115the townsite (there was no other feeding of deer during our study). Observations near dawn and dusk at a
116feed block began two days after deer discovered it. Thereafter, blocks were covered and unavailable to
117deer except during observations. At the start of each observation we placed next to the block a 10 cm-
118diameter petri dish containing 10 mL of Terra-sorb hydrogel (Garden Harvest Supply, Berne, IN, U.S.A.)
119and 15 mL of either deionized water or coyote urine (PredatorPee.com). These treatments were alternated
120between successive 2-h observations at each site. Deer behaviors were spoken into a voice recorder, and
121JWatcher 1.0 (Blumstein and Daniel 2007) was used to calculate the time that each individual deer
122(identified by distinctive scars or other features) spent feeding during the first minute after it had
123approached within 10 m of the feed block.

124***Habitat and plant species preferences, and spatial distribution of preferred habitats and species***

125During 2011 scan samples we recorded whether deer were sighted in open forest, open dry meadow, or
126wet meadow with willows. To estimate habitat preferences we compared habitat-specific sighting
127frequency to that expected if deer were observed in proportion to areas of these habitats within the
128viewsheds of scan points or route segments. To determine if the availability of the three habitats varied
129with distance from the Gothic townsite, we calculated the proportion of the viewshed visible from each
130point or route segment that consisted of each habitat. We then regressed those proportions on distance of
131the scan point or segment midpoint from the most peripheral summer-occupied RMBL building (hereafter
132“nearest cabin”). Mapping of viewsheds as described above ensured that detectability of deer was
133equivalent across habitats.

134 To characterize palatability of plants we sampled 15 m of line transect in summer 2005 in each of
1359 meadows containing blue columbine (*Aquilegia coerulea*), a plant often browsed by deer around the
136RMBL (personal observations). For every non-graminoid herbaceous plant (forb) that intersected the
137transect line we recorded whether any shoots had been clipped by deer (small mammals clip much closer
138to the ground and take much smaller bites than deer), using the proportion of all individuals of a species
139at a site with at least one clipped shoot as a measure of the intensity of deer herbivory of that species. We

140 augmented these measures in 2010 with 18 m of line transect near the center of each of the viewsheds
141 scanned for deer activity during that summer. We sampled these as described for 2005 transects, except
142 that herbivory was expressed as the proportion of all shoots of intersected plants that were clipped, rather
143 than as the proportion of individuals that had at least one shoot clipped. Finally, we pooled 2005 and
144 2010 data, and from them derived an index of preference (= palatability) for each species as the mean
145 proportion clipped across the 14 sites sampled by transects. Graminoids (grasses and sedges) are so
146 rarely eaten by mule deer (personal observations) that we assumed their clipping rates were zero.

147 To see if the abundance of palatable plants varied with distance from the townsite we established
148 a single 50-m line transect laid out in random compass orientation in the center of each of the 24 scan-
149 point viewsheds observed in 2011. We lowered a stiff wire “pin” every 1 m along these transects and
150 identified all plants touched by the pin, as well as bare ground if no plant was touched. This standard
151 “point intercept” method can be used to characterize canopy cover of vegetation as a whole, or of
152 individual plant species or groups of species. We estimated overall vegetation cover by dividing the
153 number of plant contacts by the total number of pindrops (50 per transect); the proportion of vegetation
154 contacts that consisted of palatable forbs by dividing total forb contacts by total vegetation contacts; and
155 the proportion of vegetation contacts that consisted of unpalatable graminoids by dividing total graminoid
156 contacts by total vegetation contacts.. Finally, we derived an index of palatability for each site by
157 multiplying the relative cover of each species (contacts of that species divided by total vegetation
158 contacts) times that species’ palatability.

159 ***Spatial gradients in herbivory and correlation with deer activity***

160 We pooled data from plant transects at the 9 sites sampled in 2005 and 5 sampled in 2010 to ask whether
161 intensity of herbivory showed any spatial pattern. We first eliminated species with low palatability (those
162 with <10% of shoots clipped on average), because including them necessarily lowers the slope of any
163 spatial trend, making it harder to detect. We also eliminated species recorded at only one site. Then, for
164 each transect, we subtracted each remaining species’ overall mean clipping proportion in the pooled

165dataset from the transect-specific value. We regressed these “residuals” on the distance of each site from
166the nearest cabin.

167 We augmented these data in 2013 with measures of deer browsing of a highly-preferred species,
168aspen sunflower (*Helianthella quinquenervis*). Over a 2-d period we located 56 patches of flowering
169sunflowers inside and outside of the Gothic townsite. In each patch we counted all browsed and
170unbrowsed flowering stalks within a circular plot of 5-m radius and regressed the proportion of stalks
171browsed against distance of the center of each plot from the nearest cabin.

172 Finally, in 2010 we estimated deer activity in the same sites that contained plant transects. For
173this year we could ask whether residual herbivory values in the transects (described above) were
174positively correlated with deer activity in the surrounding viewsheds.

175***Effects of deer herbivory on two palatable wildflower species***

176We estimated the impact of deer herbivory on reproduction and seedling recruitment for two additional
177preferred native species, blue columbine (*A. coerulea*) and scarlet gilia (*Ipomopsis aggregata*). In
178summer 2005 we chose 3 pairs of columbine plants at each of two locations, one ca. 1 km north of the
179townsite and one within the townsite. Plants were paired by stature and number of flower buds, and one
180chosen at random was caged to exclude deer but not pollinators. At the end of summer we counted fruits
181on all plants and left them intact to disperse seeds. In summer 2006 we returned to locate all seedlings
182within 50 cm of each 2005 study plant; these plants were sufficiently isolated from one another, and seeds
183fall sufficiently close to the parent, that assignment to parent was unambiguous. For scarlet gilia we can
184draw on our own extensive previous studies at the RMBL to assess effects of deer herbivory on seed
185production and seedling recruitment.

186***Spatial and statistical analyses***

187A Garmin 12 GPS unit provided map locations of coyote scat, aspen sunflower patches, and deer survey
188points. ArcMap 10/ ArcInfo software (ESRI, Redlands, CA, USA) allowed us to overlay points and
189viewshed/habitat boundaries onto high-resolution aerial photographs of the East River Valley and to
190analyze distances, viewshed areas, and habitat distributions.

191 We evaluated the hypothesized spatial gradient in coyote activity (Fig. 1) in two ways. For the
192 first measure—coyote sightings near marmot colonies—we regressed total sightings per hour of
193 observation at a colony on viewshed area for that site and distance from the nearest cabin at RMBL.
194 Viewshed area had no effect, perhaps because it varied little among sites, so we dropped it from the model
195 and regressed sightings per hour on distance. For the second measure—coyote scat per m of trail— we
196 drew isolines at increasing distances from the nearest cabins (Fig. 2) and calculated total m of trail walked
197 in each distance interval for 2011, 2012, and 2013. We then pooled data across summers and regressed
198 scat per m of trail against the midpoint of each distance interval. A Chi-squared goodness-of-fit test
199 showed whether scat numbers were proportional to m of trail walked at each distance.

200 To evaluate the predicted spatial gradient in deer activity (Fig. 1) we first analyzed data from
201 2010 and 2011 separately and then combined probabilities across the two years to assess the overall
202 statistical strength of any distance effect. For each year, we did preliminary factorial ANCOVAs with all
203 possible effects and used backwards elimination to simplify the models. To visualize any distance effect,
204 we then took residuals from models with distance removed, and regressed the residuals on distance from
205 the nearest cabin. In 2010 only viewshed area and distance were important and they did not interact, so
206 we could express activity as deer seen per scan per viewshed area. In 2011 viewshed area, distance, and
207 their interaction all were significant, so we expressed activity as residuals from a model of deer per scan
208 as a function of viewshed area and its interaction with distance from the nearest cabin. In no case were
209 residuals from final models heteroscedastic or non-normal.

210 To analyze the relationship between deer activity and herbivory (Fig.1) we regressed residual
211 herbivory rate, treating species residuals as nested within sites, against the site's distance from the nearest
212 cabin. For 2010 we also had information on deer activity from scan samples in the viewshed around plant
213 transects, and so could ask whether residual herbivory rate varied with deer activity. Again, we examined
214 all residuals and found no need to transform raw variables.

215

216 **Results**

217 *Spatial gradients in activity of coyotes and deer*

218 Two different metrics indicate that coyotes avoid the Gothic townsite, as predicted (Fig.1). First, 148
219 coyotes were recorded during 7,865 hours of marmot observations in the East River Valley over the 9
220 summers between 2002 and 2010. Of these, 7 were seen at marmot colonies within the townsite, 39 at a
221 colony ca. 500 m south, and 102 at four colonies 1300–3500 m north. Total sightings per hour increased
222 with distance of the viewshed centroid from the nearest cabin (Fig. 3A; $F_{1,4} = 14.98$, $P = 0.018$, $R^2_{\text{adj}} =$
223 0.74). Second, of 178 coyote scats mapped in 2011, 2012, and 2013, the number per 100 m of trail
224 increased with distance from the townsite, based on midpoints of trail segments < 250 m, 250–500 m,
225 500–750 m, and > 750 m from the nearest cabin (Fig. 3B; ANCOVA with year as random effect and
226 distance as covariate, $F_{1,8} = 5.18$, $P = 0.052$ for distance effect, insignificant year \times distance interaction,
227 $R^2_{\text{adj}} = 0.49$). There were about half as many scats < 250 m from the townsite as expected from the relative
228 lengths of trail walked at that distance vs. the others ($X^2 = 18.13$, $df = 3$, $P < 0.005$).

229 In contrast to coyotes, does were especially apparent in the Gothic townsite, as predicted by the
230 trophic cascade hypothesis (Fig.1). In 2010 the number of deer observed per scan per ha of viewshed
231 tended to decline with distance of the centroid of the viewshed from the nearest cabin ($F_{1,4} = 1.84$, $P =$
232 0.25, $R^2_{\text{adj}} = 0.14$). Any pattern is due entirely to does (Fig. 4A; $F_{1,4} = 2.41$, $P = 0.20$, $R^2_{\text{adj}} = 0.22$) rather
233 than bucks (Fig. 4A; $F_{1,4} = 0.02$, $P = 0.89$, $R^2_{\text{adj}} = -0.24$; this negative value indicates a poor model fit), as
234 predicted under the trophic cascade hypothesis. Turning to 2011, preliminary ANOVA showed that the
235 way deer were sighted (whether during a point scan or while walking a route segment) did not influence
236 the number seen, so we pooled point and segment sightings. Deer sightings decreased with distance of
237 the scan point or segment midpoint to the nearest cabin and increased with viewshed area, but in contrast
238 with 2010, the area effect was smaller at long distances ($F_{1,45} = 11.76$, $P < 0.001$; $F_{1,45} = 49.34$, $P <$
239 0.0001; $F_{1,45} = 6.87$, $P < 0.012$ for Distance, Area, and their interaction, respectively; model $R^2_{\text{adj}} = 0.51$).
240 Does again dominated this pattern (Fig. 4B, $F_{1,45} = 9.59$, $P = 0.003$; $F_{1,45} = 38.52$, $P < 0.0001$; $F_{1,45} = 4.49$,
241 $P < 0.04$ for Distance, Area, and their interaction, respectively, $R^2_{\text{adj}} = 0.45$). In contrast to 2010, activity
242 of bucks in 2011 did decline away from the townsite (Fig. 4B, $F_{1,45} = 5.15$, $P = 0.028$; $F_{1,45} = 24.62$, $P <$

2430.0001; $F_{1,45} = 5.29$, $P < 0.03$ for Distance, Area, and their interaction, respectively, $R^2_{adj} = 0.32$).

244However, a difference between the sexes becomes clear when we consider results from both summers
245together: the overall decline in activity with distance from the townsite is highly significant for does (X^2
246= 16.51, $df = 4$, $P = 0.002$; combined probability after Fisher 1970, pp. 99–100) but not for bucks ($X^2 =$
2477.38, $df = 4$, $P = 0.12$).

248*Behavioral response of deer to coyote urine*

249Does were more vigilant when they encountered a stimulus that suggests coyote presence. In 58 h of
250observation in 2011 we observed 86 individual does in the vicinity of feed blocks; of these, 22
251approached blocks paired with coyote urine and 9 approached blocks paired with water. Differential
252approach to urine ($X^2 = 5.45$, $d.f. = 1$, $P = 0.02$) suggests investigation of a potentially-important cue, and
253does allocated significantly less time to foraging in the first minute following their approach to blocks
254with urine (11.9 s on average vs. 23.5 s for deer approaching control feed blocks; $F_{1,31.02} = 4.96$, $P = 0.033$;
255linear mixed-effects model).

256*Habitat and plant species preferences, and spatial distribution of preferred habitats and species*

257Neither habitat nor food preference provides an alternative explanation for the spatial gradient in activity
258of does and fawns. Proportions of forest, dry meadow, and wet meadow—the three main habitats in
259viewsheds scanned for deer in 2011—did not vary significantly with distance from the nearest cabin
260(linear regressions, $P > 0.75$ for each habitat type). Similarly, based on transects surveyed in 2011 at each
261of the 24 deer survey points (Fig. 2), overall vegetation cover, proportion of vegetation hits to graminoids
262(grasses and sedges, which mule deer rarely or never eat), and proportion of vegetation hits to forbs (non-
263graminoid herbs, some of which they eat) did not vary significantly with distance (for total vegetation
264cover, graminoid proportion, and forb proportion respectively, $F_{1,22} = 1.22$, $P = 0.28$, $R^2_{adj} = 0.01$; $F_{1,22} =$
2651.45, $P = 0.24$, $R^2_{adj} = 0.019$; $F_{1,22} = 1.05$, $P = 0.32$, $R^2_{adj} = 0.002$). The mean palatability of the forbs in
266each transect (values in Table 1 weighted by relative cover of each species) also did not vary with
267distance to the nearest cabin ($F_{1,22} = 0.34$, $P = 0.57$, $R^2_{adj} = 0.034$). Second, and in any case, does
268exhibited no strong habitat preference. Of 87 does seen in 2011, 19 (22%) were in forest, 62 (71%) in dry

269meadow, and 6 (7%) in wet meadow. These values do not differ significantly from the representation of
270forest (19%), dry meadow (68%) and wet meadow (13%) in 2011 viewsheds ($X^2 = 3.03$, $df = 2$, $0.5 > P >$
2710.1). Bucks, in contrast, preferred forest: of 29 seen in 2011, 12 (41%) were in forest, 15 (52%) in dry
272meadow, and 2 (7%) in wet meadow ($X^2 = 9.65$, $df = 2$, $P < 0.01$).

273***Spatial gradients in herbivory and correlation with deer activity***

274As predicted (Fig. 1), shoots of palatable plant species were less likely to be eaten the farther a transect
275was from the nearest cabin (Fig. 5A; $F_{1,78} = 3.86$, $P = 0.053$, $R^2_{adj} = 0.04$). Considerable scatter reflects the
276fact that we included species differing greatly in their palatability. Proportional consumption of flowering
277stalks of a single highly-palatable species, aspen sunflower (*Helianthella quinquenervis*), declined much
278more distinctly with distance from the nearest cabin in 2013 (Fig. 5B; $F_{1,55} = 16.45$, $P = 0.0002$, $R^2_{adj} =$
2790.22).

280 We can also relate the proportion of clipped forb shoots in 2010 transects to estimates of deer
281activity in each transect's viewshed. These measures are positively correlated (Fig. 6, $F_{1,26} = 5.73$, $P =$
2820.024, $R^2_{adj} = 0.15$), again as predicted.

283***Effects of deer herbivory on two palatable wildflower species***

284Deer herbivory greatly reduced the seed production and seedling recruitment of two palatable native
285wildflowers. Compared to blue columbine (*Aquilegia coerulea*) plants that were caged to exclude deer,
286uncaged plants produced on average < 30% as many mature fruits (least-squares means of 5.33 vs. 18.50
287fruits, $F_{1,10} = 10.60$, $P = 0.009$). Estimating from counts of seeds per fruit vs. fruit size on plants not used
288in the experiment, uncaged plants produced < 40% as many seeds as caged plants (means of 990 vs. 2563
289seeds, $F_{1,10} = 4.02$, $P = 0.073$). These differences carry through to the next stage of the life cycle: in 2006
290only about 16% as many seedlings emerged within 50 cm of columbines that were uncaged in 2005 as
291emerged under caged ones (means of 1.0 vs. 6.1 seedlings, $F_{1,8} = 12.10$, $P = 0.008$, randomized-blocks
292ANOVA). Scarlet gilia (*Ipomopsis aggregata*) exhibits a similar effect (this species is not listed in Table
2931 as "palatable" only because it occurred in just one plant transect). In a previous study (Brody et al.
2942007) we mapped 5,324 seedlings of the species at three sites within the Gothic townsite and followed

295 these individuals through 2004 when all had flowered and died or had died without flowering. In a
296 subsample of about half of those that flowered we found that 55% had their inflorescences browsed by
297 deer. We also found (Sharaf and Price 2004) that 78 plants whose inflorescences were clipped in 1999 and
298 2000 to mimic deer damage set only 16% as many seeds on average as 112 paired unclipped plants
299 (means of 32.9 vs. 202.6 seeds, $F_{1,182} = 48.32$, $P < 0.0001$). Combining these values, we estimate that deer
300 herbivory within the townsite reduces seed set on average to only about 9% of that in unbrowsed *I.*
301 *aggregata* plants. Again these differences should carry through into the offspring life cycle, since reduced
302 seed set in this species corresponds in a linear fashion to fewer emerging seedlings and fewer individuals
303 surviving to reproduce (Price et al. 2008, Waser et al. 2010).

304

305 Discussion

306 Cascading effects of predator-prey interactions on lower trophic levels have been described less often for
307 terrestrial ecosystems, particularly those involving large mammals, than for aquatic ecosystems (Pace et
308 al. 1999; Schmitz et al. 2000). Although this difference might derive from variation among ecosystems in
309 attributes, such as the magnitude of compensatory food-web processes, that affect the strength and thus
310 detectability of cascades, other explanations are possible. Many recent reviews have focused on biomass
311 or productivity responses at the scale of whole communities, and on experimental addition or removal of
312 top predators, as the “gold standards” of evidence. Cascades can strongly affect a subset of species,
313 however, without detectable change in overall biomass or productivity of a trophic level (Polis 1999).
314 And an emphasis on experiments, which are rarely feasible for large mammals for logistic and ethical
315 reasons, can unnecessarily overlook other evidence (Pace et al. 1999; Schmitz et al. 2000). We submit that
316 alternative types of evidence often are at hand, the example here being the spatial variation in predation
317 risk that allowed us to visualize cascade processes (see also Hebblewhite et al. 2005; Harrington and
318 Conover 2007).

319 A second philosophical point is in order. We used a “case study” approach, gathering information
320 on relationships among humans, coyotes, deer, and plants from a variety of studies with different designs

321that explored different aspects of the system. Indeed, even studies of the same aspect tended to change
322from year to year, as we fine-tuned their design. Because of this heterogeneity of evidence we explored
323each link in the proposed trophic cascade separately (Fig. 1) and evaluated the overall hypothesis that a
324cascade exists by asking how consistently the results supported predicted relationships. The overall
325approach, as data from different sources accumulates, is to repeatedly update our assessment of the
326probability of the model given the totality of the data. This process is essentially “Bayesian” even
327without a formal Bayesian statistical analysis (which was not possible in our study given the
328heterogeneous evidence). It is common in ecology to instead insist on a one-step approach in which a
329biological hypothesis such as “a coyote–deer–plant trophic cascade exists” is tested via a statistical
330hypothesis such as “herbivore activity and plant consumption are equal with and without carnivores,”
331from which the resulting P value is the probability of the data given the model. But the way that humans
332—including infants and scientists—form an understanding of the natural world is “Bayesian” in the same
333sense as used above (Téglás et al. 2011), and most ecological hypotheses are in fact complex conceptual
334models (Price and Billick 2010) not properly evaluated by a single test. Although we did use a null-
335hypothesis approach to explore specific relationships, what is important is that the numerous pieces of
336evidence gathered over 12 summers of field work (2002–2013) consistently supported the model and did
337not support the alternative possibility that deer are responding to spatial gradients in preferred habitats or
338plant species rather than to predator distribution. In general, ecologists often accumulate varied clues
339about natural phenomena, and we stress that all such information can and should be used to refine and
340gain confidence in our models of nature.

341 In exactly this spirit, several pieces of natural-history evidence suggest that antipredator behavior
342contributes to the gradient in doe activity away from the townsite (mortality from coyote attack may
343contribute as well, but we have not investigated that possibility). Of all age classes, fawns are at highest
344risk of mortality from coyote predation (e.g., Lingle 2000; Pojar and Bowden 2004), and mule deer does
345choose relatively low-risk habitats in which to hide their newborn fawns (Long et al. 2009). At the
346RMBL, coyote avoidance of the townsite would not only reduce the risk to fawns, but also allow does to

347 devote less time to vigilance and more to feeding in support of energetically-costly lactation. Our
348 observation that deer feed less when they encounter coyote urine suggests that vigilance does incur a lost
349 opportunity cost, consistent with results from other ungulates (cf. Laundré et al. 2001 and references
350 therein; Conover 2007). Other studies at the RMBL also suggest that deer are more likely to pay the cost
351 of vigilance in high-risk areas. Carrasco and Blumstein (2012) found that deer in the townsite
352 discriminate between neutral and risk-associated auditory stimuli, whereas those farther away flee from
353 either stimulus as if they perceive their habitat to be risky. And several of us (submitted manuscript)
354 observed that deer alert to and flee from an approaching human sooner when the deer are farther from the
355 townsite.

356 The wide variation among plant species in palatability, and the striking effect of deer herbivory
357 on the demography of two highly-palatable species, indicate that the primary effect of the trophic cascade
358 could be to shift the species composition of the plant community toward unpalatable species (see also
359 Rooney 2001; Suzuki et al. 2012). It would be logical to address this possibility by comparing the
360 demography of palatable and unpalatable plants, and the species composition of plant communities,
361 across a gradient in deer activity. Unfortunately, we cannot yet expect a pattern in community
362 composition to be evident around the RMBL. Deer became common in the townsite only in the late
363 1980s, when the human population at RMBL reached its current self-imposed summer maximum of 160
364 persons. In contrast, any detectable changes in species composition of our subalpine plant communities
365 are likely to take many decades, because almost all of the species are long-lived herbaceous perennials
366 that do not accumulate a record of their growth history in above-ground woody tissues. Instead, their
367 abundances change slowly, through often-sporadic seedling recruitment. Furthermore, cattle also graze
368 the subalpine in the autumn, following the summer months in which we did the work described here.
369 Addressing the effect of the trophic cascade on community composition will therefore require long-term
370 monitoring with experimental exclusion of cattle as well as deer. These are challenging tasks for the
371 future.

372

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381

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437 **Figure Legends**

438

439 **Figure 1. Diagrammatic representation of the trophic cascade hypothesis, its predictions, and the**
440 **evidence brought to bear in this study.** The cascade (left) links adjacent trophic levels via indirect
441 (dashed lines) and direct (solid lines) negative effects. If this cascade exists we predict (center) a series of
442 spatial relationships (dotted lines) between human activity and coyote activity, between coyote activity
443 and activity of does and fawns, and between deer activity and plant reproduction. Diverse pieces of
444 evidence (right) all support the predictions.

445

446 **Figure 2. The Gothic townsite and surrounding landscape.** Buildings are black polygons. Blue lines
447 trending north-south and east-west are rivers; yellow lines are main trails and roads. Rounded black lines
448 are isolines 250, 500, and 750 m from the most peripheral summer-occupied cabins. Green and red
449 circles are centroids of viewsheds scanned for deer in 2010 and 2011, respectively. Coyote scats were
450 collected along trails and roads, and coyote sightings were recorded at marmot colonies (not shown)
451 inside and outside of the townsite.

452

453 **Figure 3. Coyote activity as a function of distance from the townsite.** (A) Coyote sightings at marmot
454 colonies. (B) Distribution of coyote scats along main trails and roads in three summers. Lines are best-fit
455 least-squares linear regressions. Predictions are for sightings and scats to increase with distance from the
456 Gothic townsite.

457

458 **Figure 4. Deer activity as a function of distance from the townsite.** (A) 2010 surveys for does and
459 bucks, expressed as deer seen per scan per ha of viewshed. (B) 2011 surveys, expressed as residuals from
460 a model of deer per scan as a function of viewshed area and its interaction with distance from the nearest
461 cabin. Predictions are for activity of does to decrease with distance from the townsite and for no strong
462 spatial pattern in activity of bucks.

463

464**Figure 5. Deer herbivory as a function of distance from the townsite.** (A) Herbivory rate of all
465palatable species in 2005 and 2010, expressed as deviations (residuals) from species-specific mean
466clipping rates. (B) Proportion of flowering stalks clipped of the preferred species *Helianthella*
467*quinquenervis*. Predictions are for herbivory rates to decrease with distance from the townsite.

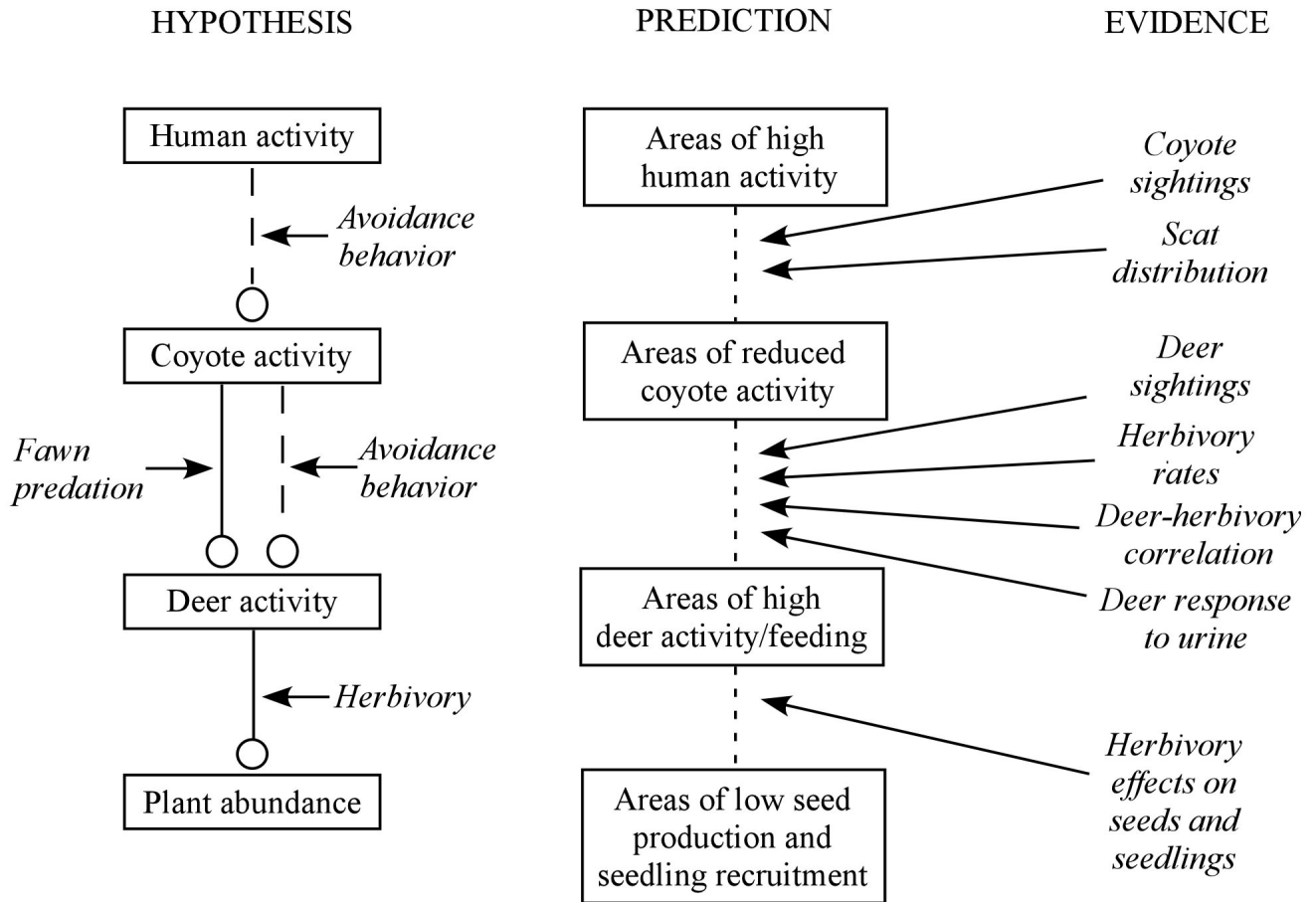
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469**Figure 6. Intensity of shoot clipping in 2010 plant transects as a function of deer activity in the**
470**surrounding viewshed.** Herbivory is expressed as the average, over all palatable species in a transect, of
471residuals from a model of proportion of shoots clipped that includes species as the only independent
472variable (Table 1). The prediction is for a positive relationship between herbivory and deer activity.

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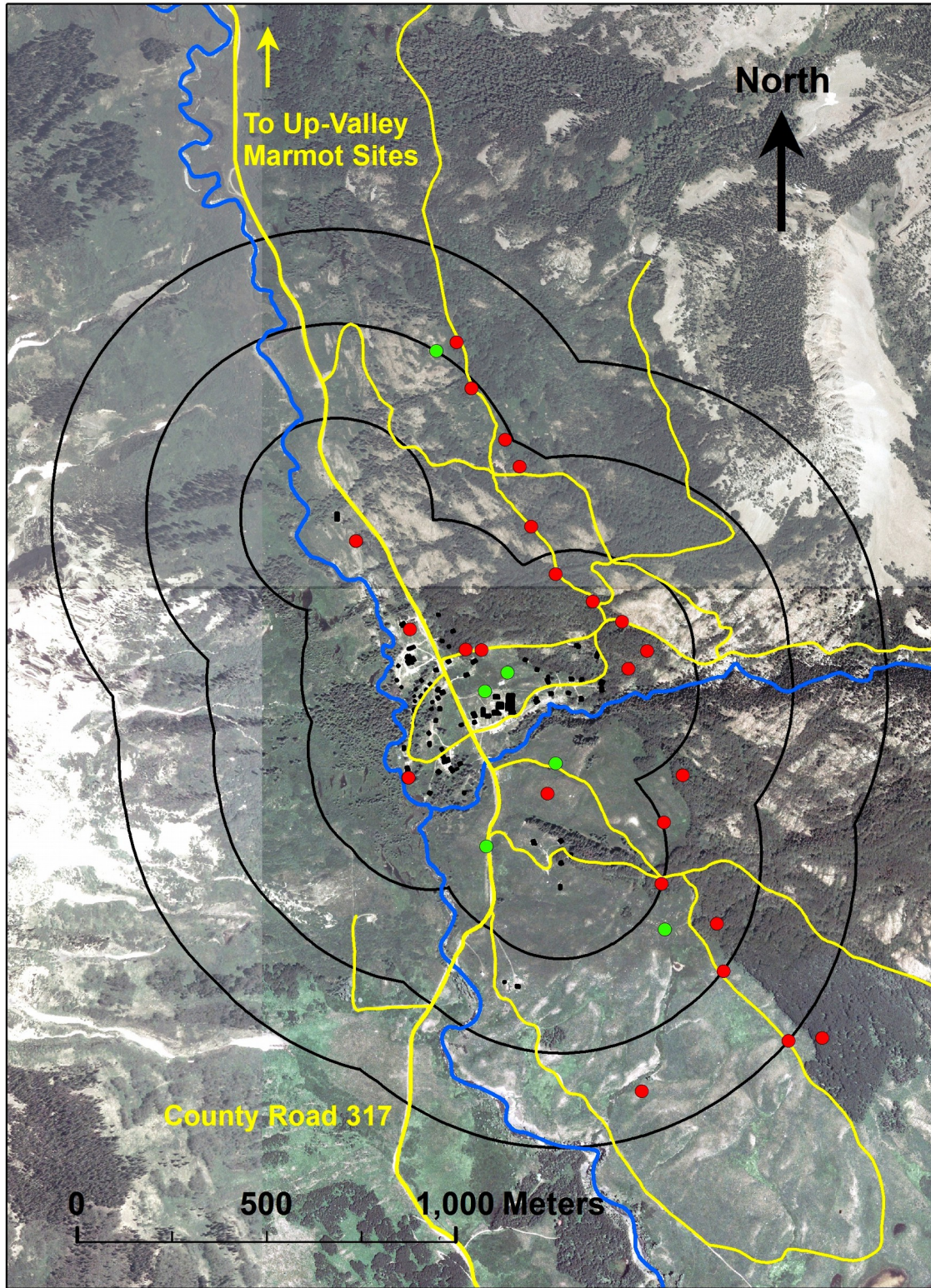
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480Figure 1.

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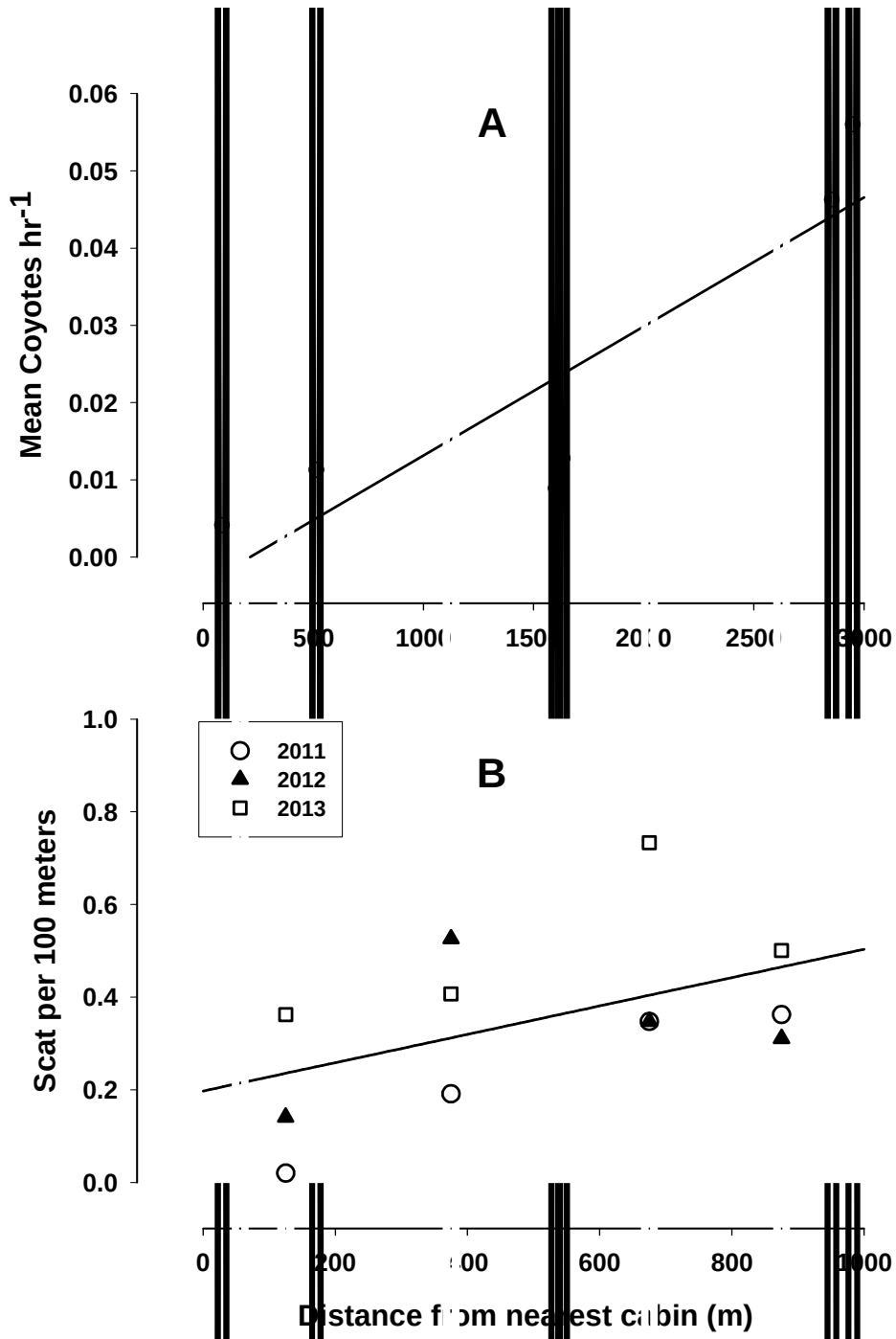


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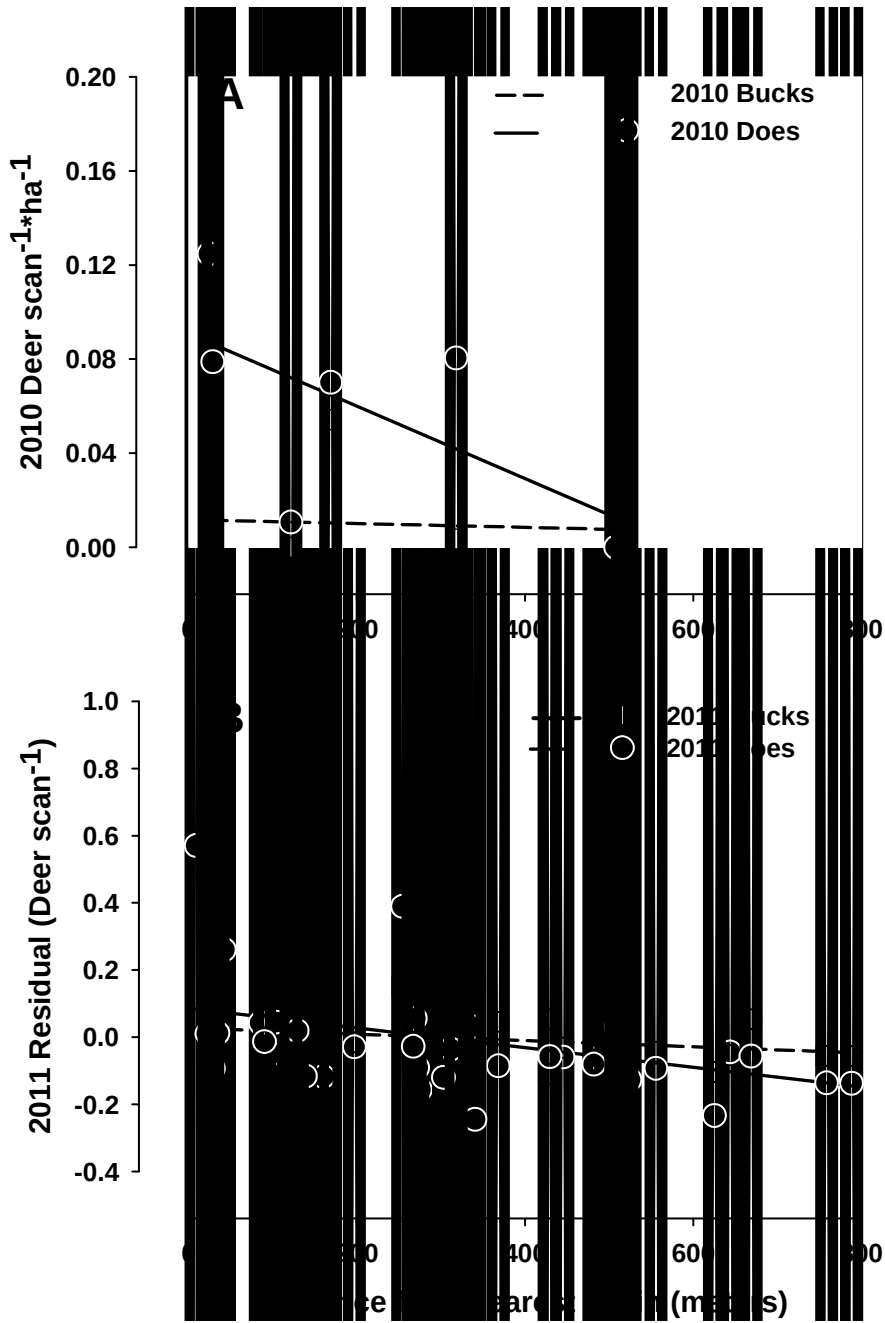
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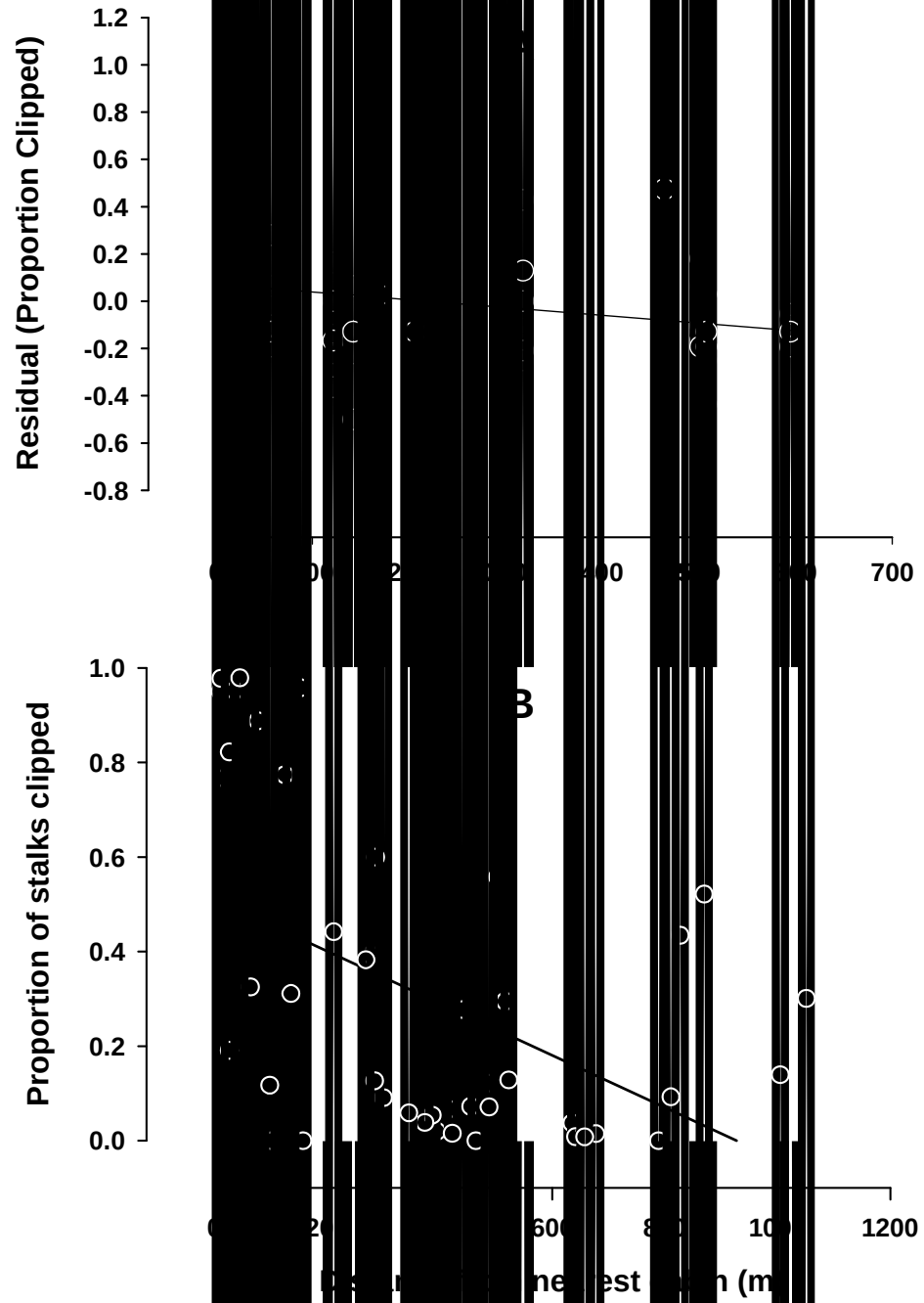
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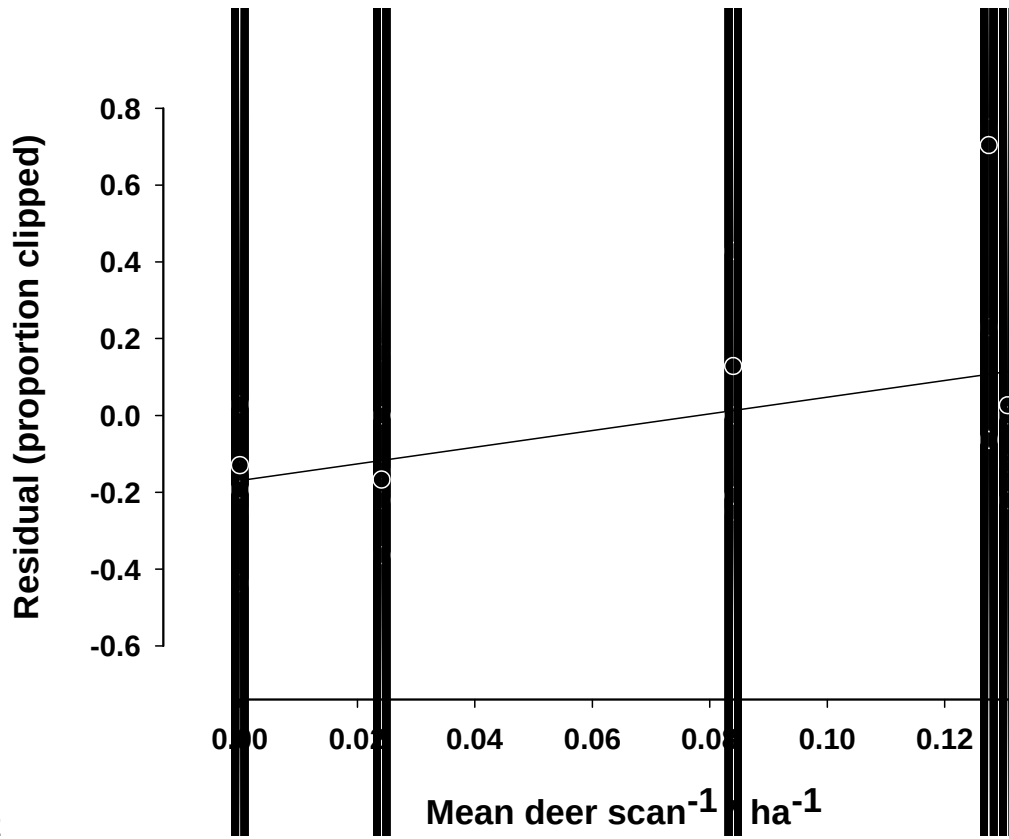
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553Figure 6.

554 **Table 1.** Palatability of forbs (herbaceous, non-graminoid plants), indicated by overall
 555 proportions of shoots clipped for each species in pooled 2005 and 2010 transects.

Species ¹	Proportion Clipped
<i>Valeriana edulis</i>	0.75
<i>Heuchera parvifolia</i>	0.64
<i>Pseudocymopterus montanus</i>	0.50
<i>Aquilegia coerulea</i>	0.44
<i>Senecio integerrimus</i>	0.33
<i>Agoseris sp.</i> ²	0.25
<i>Helianthella quinquenervis</i>	0.22
<i>Valeriana occidentalis</i>	0.19
<i>Collomia linearis</i>	0.14
<i>Viola nuttallii</i>	0.13
<i>Epilobium angustifolium</i>	0.12
<i>Solidago multiradiata</i>	0.12
<i>Geranium richardsonii</i>	0.10
<i>Potentilla pulcherrima</i>	0.07
<i>Taraxacum officinale</i>	0.05
<i>Linum lewisii</i>	0.03
<i>Delphinium barbeyi</i>	0.02
<i>Lathyrus leucanthus</i>	0.02
<i>Pedicularis bracteosa</i>	0.02
<i>Ligusticum porteri</i>	0.01

556

557¹Species in our samples that were never eaten were *Achillea lanulosa*, *Arnica cordifolia*,

558 *Artemisia dranunculus*, *Aster foliaceus*, *Campanula rotundifolia*, *Castilleja sulphurea*,

559 *Descurainia pinnata*, *Dugaldia hoopesii*, *Erigeron elatior*, *Erigeron speciosus*, *Fragaria*

560 *virginiana*, *Frasera speciosa*, *Galium septentrionale*, *Geum macrophyllum*, *Heliomeris*

561 *multiflora*, *Heracleum lanatum*, *Hydrophyllum fendleri*, *Lomatium dissectum*, *Lupinus argenteus*,

562 *Mahonia repens*, *Osmorhiza occidentalis*, *Pneumonanthe parryi*, *Rosa woodsii*, *Senecio*

563 *bigelovii*, *Senecio serra*, *Smilacina stellata*, *Thalictrum fendleri*, and *Vicia americana* Those that

564 were eaten but were recorded only at a single site were *Ipomopsis aggregata* and *Tragopogon*

565 *pratensis*.

566²Not in flower when transects were sampled, but most likely *A. aurantiaca*.