

VARIABLE RESPONSE OF BUTTERFLIES AND VEGETATION TO ELK HERBIVORY: AN EXCLOSURE EXPERIMENT IN PONDEROSA PINE AND ASPEN-MIXED CONIFER FORESTS

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ABSTRACT—Herbivory by wild ungulates influences the structure and composition of plant communities, but less is known about how such changes affect species richness and abundance of insect herbivores. In Bandelier National Monument, New Mexico, 1999 to 2002, we used ungulate exclosures and reference sites to measure the response of butterflies to herbivory by high numbers of elk (*Cervus elaphus*) in ponderosa pine (*Pinus ponderosa*) grassland and aspen-mixed conifer forests. At each site, we measured butterfly abundance, species richness, and selected environmental variables. Butterfly abundance and species richness significantly differed among dates in ponderosa pine-grassland sites and differed significantly for date, treatment, and date*treatment interaction in aspen-mixed conifer sites in 2001, the year of greatest butterfly abundance and richness. Environmental variables differed little between treatments in either habitat, with the exception of the distribution of aspen stem densities, which significantly differed among height classes and treatments in 2001 and 2002. Results of nonmetric, multidimensional scaling ordination indicated that butterfly community composition in late summer was best explained by non-woody biomass, blooming forb species richness and abundance, and aspen saplings excluded from elk in the aspen-mixed conifer sites. Although elk were only excluded for 4 y, our results indicated that, at high densities, they browse non-woody vegetation and young aspen, which in turn has a cascading affect on adult butterfly community composition in some habitats during some years.

RESUMEN—La herbivoría de los ungulados silvestres influye en la estructura y composición de las comunidades vegetales, pero se sabe menos sobre cómo esos cambios afectan la abundancia y riqueza de especies de insectos herbívoros. En Bandelier National Monument, Nuevo México, de 1999 a 2002, usamos áreas encerradas para ungulados y áreas de referencia, para medir la respuesta de mariposas a la herbivoría por un número elevado de alces (*Cervus elaphus*) en prados de pinos ponderosa (*Pinus ponderosa*) y en bosques de álamos y coníferas mixtas. En cada sitio medimos la abundancia de mariposas, la riqueza de especies, y variables medioambientales seleccionadas. La abundancia de mariposas y la riqueza de especies variaron significativamente para distintas fechas en áreas de prado de pino ponderosa, y difirieron significativamente para fechas, tratamiento, y la interacción fecha*tratamiento en áreas de álamos y coníferas mixtas en el 2001, el año de mayor riqueza y abundancia de mariposas. Las variables medioambientales se diferenciaron poco entre tratamientos en ambos hábitats, con la excepción de la distribución de densidades de troncos de álamos, que varió significativamente entre clases de altura y tratamientos en 2001 y 2002. Los resultados de la ordenación en escala multidimensional no métrica indicaron que la composición de las comunidades de mariposas en el verano tardío se explicaba mejor en términos de biomasa no leñosa, riqueza y abundancia de especies de hierbas florecientes, y álamos jóvenes excluidos de los alces en áreas de coníferas mixtas. Aunque los alces fueron excluidos por sólo cuatro años, nuestros resultados indican que en altas densidades ramonean vegetación no leñosa y álamos jóvenes, lo que a su vez tiene un efecto cascada sobre la composición de la comunidad de mariposas adultas, en algunos hábitats, en algunos años.

Numerous studies demonstrate that herbivory by wild ungulates influences the structure and composition of plant communities (e.g., Anderson and Loucks, 1979; Alverson et al., 1988; Tilghman, 1989; Tschardtke, 1997; Augustine and Frelich, 1998; Kay and Bartos, 2000). In the

Rocky Mountains of North America, browsing by large numbers of elk (*Cervus elaphus*) is inhibiting quaking aspen (*Populus tremuloides*) regeneration and altering understory herbaceous and woody species composition in some areas (Sheppard and Fairweather, 1994; Romme et al., 1995; Allen, 1996; Baker et al., 1997; Kay, 1997; White et al., 1998; Kay and Bartos 2000; Ripple and Larsen, 2000; Kay, 2001). Effects that result from a hyperabundance of ungulates has been attributed to a trophic cascade resulting from the loss of top-down regulation of ungulates by large predators (Tscharntke, 1997; Ripple et al., 2001; Terborgh et al., 2001). Within U. S. Department of Interior, National Park Service units, these impacts might be further intensified due to lack of hunting pressure.

Because herbivory by wild ungulates alters plant structure and composition, changes in the diversity and abundance of insect herbivores that use the same plant resources are to be expected (Tscharntke, 1997; Rambo and Faeth, 1999; Bailey and Whitham 2002). Incidental predation, competition for host plant resources, or physical alterations of hostplants (e.g., palatability) or habitat (e.g., light intensity) are all factors that potentially affect insect richness and abundance (Tscharntke, 1997).

Most studies examining the effects of ungulate grazing and browsing on invertebrates have focused on the effects of domestic livestock grazing in Europe and North America (e.g., Thomas, 1980; Oates, 1995; Feber et al., 2001; WallisDeVries and Raemakers, 2001; Gómez and González-Megías, 2002). Few studies have examined effects of wild ungulate browsing on insects, in particular on Lepidoptera (Baines et al., 1994; Pollard and Cooke, 1994; Feber et al., 2001; Bailey and Whitham 2002). Moreover, results of these studies vary considerably as to the positive versus negative effects of wild ungulate herbivory on insect herbivores (Feber et al., 2001; Stewart, 2001). Feber et al. (2001) indicated that 75% of resident butterflies in the United Kingdom are reliant on vertebrate grazers to maintain open conditions in grasslands and early successional habitats in woodlands and that effects vary depending on the species and its habitat. In Scotland, Baines et al. (1994) used exclosures to study effects of red deer (*C. elaphus*) grazing on invertebrates and found numbers of Lepidoptera larvae (moths) to be 4 times greater within exclosures than in grazed areas. They attributed

this primarily to removal of hostplant biomass and leaf tips by grazing, and secondarily to tree density and rainfall. In England, Pollard and Cooke (1994) found that herbivory by large numbers of Muntjac deer (*Muntiacus reevesi*) reduced the lower leaves of honeysuckle (*Lonicera periclymenum*), which are potential oviposition sites for white admirals (*Ladoga camilla*).

In North America, Rambo and Faeth (1999) examined effects of native elk and deer and domestic cattle grazing on insects. They found that insect species richness (based on morphotypes) did not differ among grazed and ungrazed habitats, but that insect abundance increased 4 to 10 times in ungrazed vegetation. Because they found plant species richness to be greater in grazed areas, they inferred that differences in insect abundance were due to differences in plant biomass and structural complexity. Most recently, Bailey and Whitham (2002) examined the effects of fire, elk herbivory of aspen, and their interaction on arthropods. They found that arthropod species richness and abundance on aspen varied depending on the severity of fire and browsing, with the greatest decreases in arthropod numbers and richness occurring where the interaction of high burn severity and elk browsing was greatest.

In the Jemez Mountains of New Mexico, numbers of elk have exponentially increased in the past 50 y (Allen, 1996). Elk presence was considered low to moderate ca. 1150 to 1500 CE (Allen, 1996; Truett, 1996) and historical observations suggest that elk were scarce before being extirpated ca. 1900 (Henderson and Harrington, 1914; Findley, 1987). In 1948, the New Mexico Department of Game and Fish released 21 cows and calves and 7 bulls of Rocky Mountain elk (*C. e. nelsoni*) into the Jemez Mountains (Keefe, 1948). From an estimate of 200 animals in 1961, the population grew to 6,000 to 8,000 individuals (10/km²) by 1989 (Allen, 1996).

In the early 1990s, the increase in elk numbers raised concerns from the National Park Service due to the considerable damage elk can inflict on plants, particularly quaking aspen, by eating the bark in winter or by direct browsing of regenerating shoots (DeByle, 1985). In Bandelier National Monument (Bandelier NM), Allen (1989) documented significant debarking of aspen by elk and browsing of sprouts after fire. In 1998, Bandelier NM deployed an array of

replicated and randomized ungulate exclosures to evaluate potential effects of elk browsing and trampling on vegetation and soil (Fettig, unpublished data). Given the management concerns of the Bandelier NM staff and lack of information on the potential effects of wild ungulates on butterflies in North America, we used the exclosures to evaluate the response of butterflies to the absence of elk herbivory.

We used butterflies to measure the effects of ungulate herbivory upon invertebrate herbivores because one or more life stages of butterflies (egg, larva, pupa, or adult) might depend on a specific plant species, plant family, or part of a plant for food or shelter. Butterflies also are considered by some to be useful biological indicators, because they are sensitive to environmental change, relatively well known, and easy to monitor (Erhardt, 1985; Erhardt and Thomas, 1991; Kremen, 1992; New et al., 1995). We also found it timely to measure the response of butterflies to elk grazing as debate continues about managing high densities of elk while balancing biodiversity protection with visitor recreation in protected western lands. In addition, the question remains as to how far top-down effects of ungulate regulation cascade to affect non-mammalian herbivores.

METHODS—Study Area and Design—We conducted our study in the ponderosa pine (*Pinus ponderosa*) grasslands and aspen-mixed conifer forests of Bandelier NM, New Mexico (Fig. 1). Elk use both plant communities in Bandelier NM (Allen, 1996). Sites were chosen in 1997 by randomly selecting 5 study areas in each plant community for placement of ungulate exclosures and reference areas. Selection criteria for placement of each site included an 80-m $\times$ 140-m rectangle of land area with less than a 15° average slope. For each area, a coin was flipped to determine which end would become the exclosure. Each exclosure encompassed one 60-m $\times$ 60-m area (0.36 ha) and was constructed of 3-m high, 10-cm grid, wire fencing attached to 3.5-m high steel posts embedded in cement. The fence excluded native ungulates and allowed for passage of small mammals, birds, and insects. Each pair was separated by a minimum of 20 m. All replicates were completed by 1 September 1998.

Aspen-mixed conifer (MC) forest sites were located within elevations of 2,700 to 2,900 m, with a conifer cover of *Pseudotsuga menziesii*, *Abies concolor*, *Pinus ponderosa*, and *P. flexilis* and some quaking aspen. Ponderosa pine grassland (PG) sites were located within elevations of 2,000 to 2,400 m and had an open *P. ponderosa* overstory, with a *Quercus gambelii* and grass-forb understory. Each site was identified by a code: MC or PG and 1 to 5 exclosure or reference, e.g., MC1ref. We used all 5 MC sites and 4 of the PG sites. We did not

sample PG5 because it was physically inaccessible during our sampling schedule. Sites MC1, MC3, MC4, and MC5 had not been burned since the 1800s, and MC2 was burned by the Cerro Grande wildfire, May 2000. Sites PG1, PG2, PG3, and PG4 were burned in the La Mesa wildfire of 1977. Sites were also burned by prescribed fire; PG1 in 1999, PG2 in 1945 and 1997, and PG4 in 1997.

Butterfly Monitoring—We monitored adult butterflies in exclosures and reference areas during the summers of 1999 to 2002 with a modified Pollard-Yates visual observation technique (Pollard and Yates, 1993). Each sample consisted of a team (1 to 2 observers and 1 tabulator) walking a continuous 10-m wide belt-transect to form one zigzag, 360-m long transect within each 0.36-ha sampling area. All butterflies observed within 5 m to each side, above and in front of the observer(s) were identified to species, except within the superfamily Hesperioidea due to the difficulty of identifying species. Each transect was timed and walked at a steady pace to maintain equivalent time intervals, and care was taken to avoid repeat counts of the same individual. Butterflies were monitored between 0800 to 1400 h, with average temperatures ranging from 18.3 to 26.0°C and wind speeds <3.0 km/h, with gusts not exceeding 4.8 km/h as determined by a Kestrel 2000 Pocket Weather Meter (Nielsen-Kellerman Co., Boothwyn, Pennsylvania). Butterfly taxonomy followed Opler (1999).

The number of butterflies and number of species observed were counted for each 360-m transect. The mean ($\pm$ SE) number of butterflies and species per 0.36 ha, and the total number of species were calculated for each plant community, for each sampling period. Paired sites were sampled on the same day, with replicates within the same sampling period monitored on the same or consecutive day for each habitat. Sampling periods were a minimum of 8 days apart. Surveys were conducted twice in June 1999 to coincide with the first brood flights and blooming of early summer forbs (pre-summer rainy season). In 2000, surveys were conducted once each in June and August. Sampling was limited due to drought-like conditions and closing of study areas as a result of the Cerro Grande fire. In 2001, surveys were conducted 4 times, 2 June through 12 August, with a 2-week break in July (5 through 19 July) to accommodate rain and emergence of species with a mid-summer flight period. In 2002, we conducted 7 surveys in MC sites and used 5 (18 June through 5 August) for analysis. This was due to an absence of butterflies, which likely resulted from the drought-like conditions. PG sites were not surveyed in 2002.

Vegetation Monitoring—We used the line-intercept method to monitor vegetation cover along 2 parallel, 50-m transects in each exclosure and reference area of both plant communities. Transects were randomly placed, but were at least 5 m from each other or the fence line. From 15 August to 15 October 1999 and 2000, basal intercept and aerial cover were measured to the nearest 1 cm to estimate total cover for each species and cover type. Cover types included bare ground, cactus, forb, grasses and sedges, organic litter, fungus, cryptogamic soil, shrub, subshrub (woody

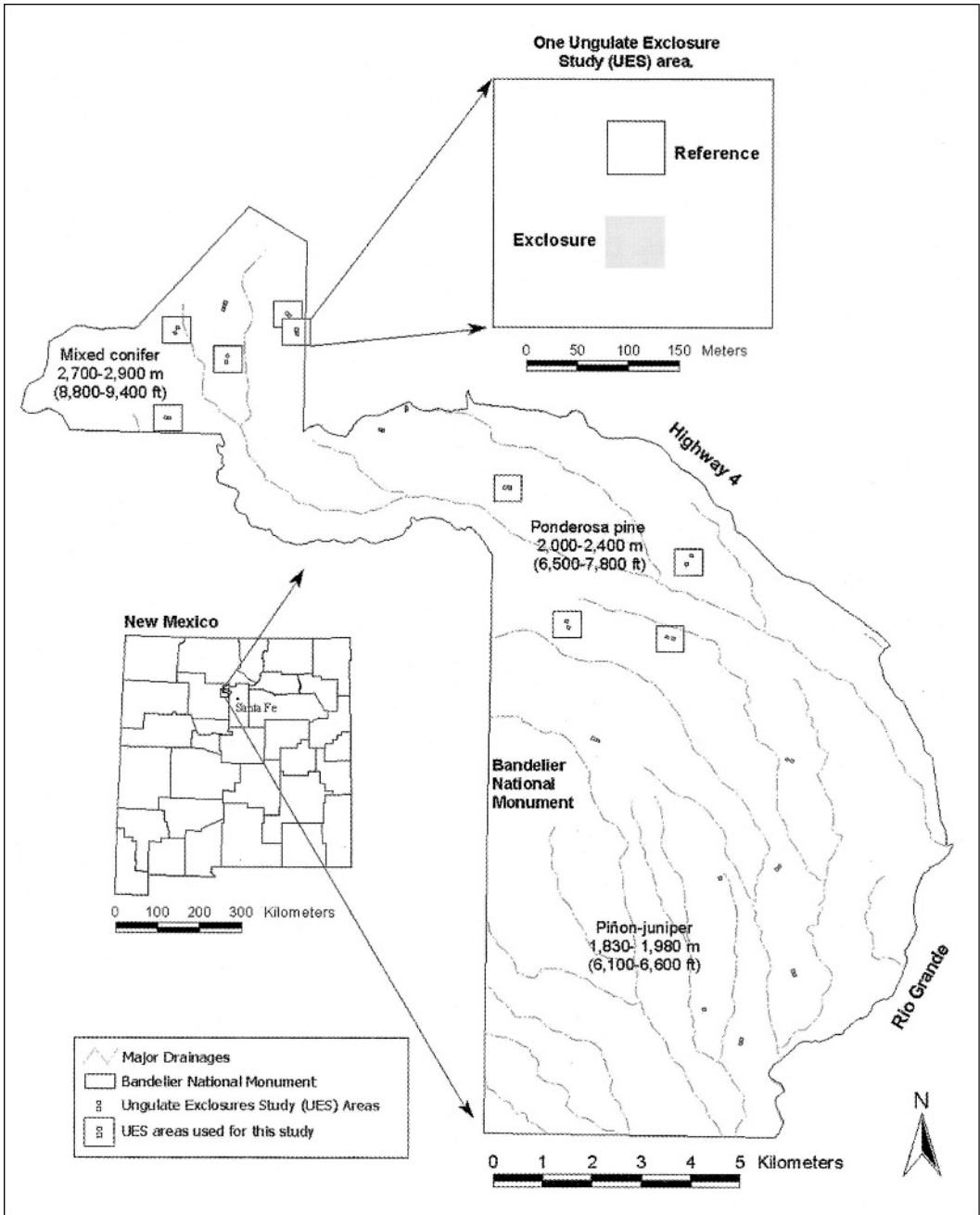


FIG. 1—Map of ungulate exclosure study areas in Bandelier National Monument, New Mexico.

perennial forbs, e.g., snakeweed, *Gutierrezia sarothrae*), tree, and unspecified.

In 2001, vegetation cover was not measured due to weaknesses associated with the line-intercept method, such as missing uncommon or clumped species and poor sampling of forb richness cover. Instead, we focused on methods that would measure variables most

associated with adult butterflies (e.g., nectar plants) or visible differences of elk browsing (e.g., aspen saplings). After each butterfly monitoring session, we immediately revisited each site and did presence-absence surveys of all blooming forbs in each of 30 randomly placed, 1-m diameter, circular quadrats. Frequency of occurrence for each blooming forb and

the species richness of blooming forbs were calculated for each site.

In MC sites, we measured the height, density, and percent canopy cover of regenerating aspen, and the percent cover of non-woody biomass in August 2001 and 2002. This was done due to measurable differences in butterfly numbers in exclosures later in the summer and to a greater presence of elk in the aspen-mixed conifer forest. We counted and measured the height of each aspen stem within each MC site. Stems were measured within the following height categories: 0.0–0.5 m, 0.51–1.0 m, 1.01–1.5 m, 1.51–2.0 m, and at 1.0-m intervals thereafter. We measured the production of non-woody biomass within 0.25-m² randomly placed quadrats at each site. Forbs and grasses were clipped and placed in separate brown paper bags at time of collection. Bags and contents were dried at 48.8°C for 24 h prior to weighing. Between 9 and 36 samples were collected at each location, with mean weight (grams) and *SD* calculated for each site. Canopy cover was estimated with a GRS densiometer (Geographic Resource Solutions, Arcata, California). Using a randomized start, we measured an index of canopy cover on a scale from 0 (none) to 4 (full cover). For each site, the sum of the 36 indices/144 was used as an index of percent open canopy cover.

Elk Monitoring—To determine seasonal elk distributions in our study areas and the eastern Jemez Mountains, we used aerial radiotelemetry surveillance data provided by Bandelier NM. Data were collected from approximately 90 elk and represented 1,479 elk locations collected on 7 flight-days, February through March, and 7 flights, April through September 2001 (Fettig, unpubl. data.).

Data Analyses—Butterfly abundance and species richness were analyzed separately for each year with a repeated measures 2-way analysis of variance test (ANOVA) to compare means between treatment, sample dates, and their interaction. Data not meeting the assumptions of ANOVA were analyzed with separate Wilcoxon sum rank tests for date and treatment effects. Our purpose was to compare samples within each year rather than pooling data and comparing among years, because the latter could potentially mask within-season temporal variation. Because 2001 was an “invasion” year for high numbers of the butterfly, *Vanessa cardui*, we did additional ANOVAs with *V. cardui* excluded to test for possible swamping effects.

We used paired *t*-tests to compare mean proportions of cover for each vegetation type of sites in 1999 and 2000 and blooming forb richness and frequency of occurrence in 2001. Paired *t*-tests were used to compare mean dry weight (grams) of grass and forb biomass and percent canopy cover. Goodness-of-fit tests were used to compare the frequency of aspen sprouts in each height class between treatments in aspen-mixed conifer sites, 2001 and 2002. We used linear regression to examine the overall relation between butterfly abundance or species richness and the frequency of occurrence of blooming forbs and forb species richness across all 2001 sampling periods.

Because results of 2-way repeated measures ANOVAs of butterfly abundance and richness for treatment or date*treatment effect were only significant for the 2001

MC data, we used ordination analysis to facilitate interpretation of the results. We used nonmetric multidimensional scaling (NMS) to analyze species community structure and to explore associations for the differences with one or more measured environmental variables. We chose NMS due to its advantages over canonical and detrended correspondence analyses for analyzing ecological community relationships (McCune and Grace, 2002). We chose to use a main matrix of 13 butterfly species detected on all 10 MC sites during sampling periods III and IV ($n = 20$), the periods of detectable differences between treatments. We used a secondary matrix of the most relevant environmental variables: sample period, presence-absence of elk, grass and forb biomass, frequency of blooming forbs, frequency of *Potentilla*, forb richness, and aspen height classes {0–0.49 m, 0.5–0.99 m, and 1.00–1.5 m}. We ran a minimum of 8 trials to check for consistency in patterns and scores, and we ultimately dropped 2 outliers (MC4 and MC5 reference sites, period III). We used the following parameters for each trial: Sorenson's Distance Measure, 2-dimensional axes, 100 runs and 100 iterations, with random seed numbers, and a 0.0001 stability criterion. To test minimum stress, we evaluated plots of stress vs. iteration and stress vs. dissimilarity. The results of Monte Carlo simulations of stress in relation to dimensionality between randomized and real data also were tested. We present results of analyses for interpretation in graphical output along with the coefficients of determination for the correlations between ordination distances and distances in the original n -dimensional space for each axis. The graph was orthogonally rotated to align the greatest number of correlated environmental variables along Axis 1.

For all analyses, data were log transformed where needed to meet assumptions of ANOVA. Proportions received the squareroot arcsin transformation. Statistical analyses were conducted with MS Excel98 (Microsoft, Redmond, Washington) or SPSS 2001 (SPSS, Chicago, Illinois). Ordination analysis was conducted with PC-Ord, version 4 (MJM Software Design, Gleneden Beach, Oregon).

RESULTS—Butterfly Species Richness and Abundance—We observed a total of 1,930 butterflies in 44 species, representing 6 families (Appendix A). The greatest numbers of butterflies and species were observed in 2001. Although the total numbers of butterflies, when pooled by year for each habitat, were greater in exclosed sites in 2 of 3 y for both ponderosa pine and aspen-mixed conifer sites, mean abundance per site was only significantly different between treatments for the aspen-mixed conifer in 2001 (Fig. 2, Table 1). Results of 2-way repeated measures ANOVAs indicated that butterfly abundance and species richness differed significantly among sampling periods (date) in 2000 and 2001 in ponderosa pine sites and in 1999 and 2001 in aspen-mixed conifer sites (Table 1). Due to the

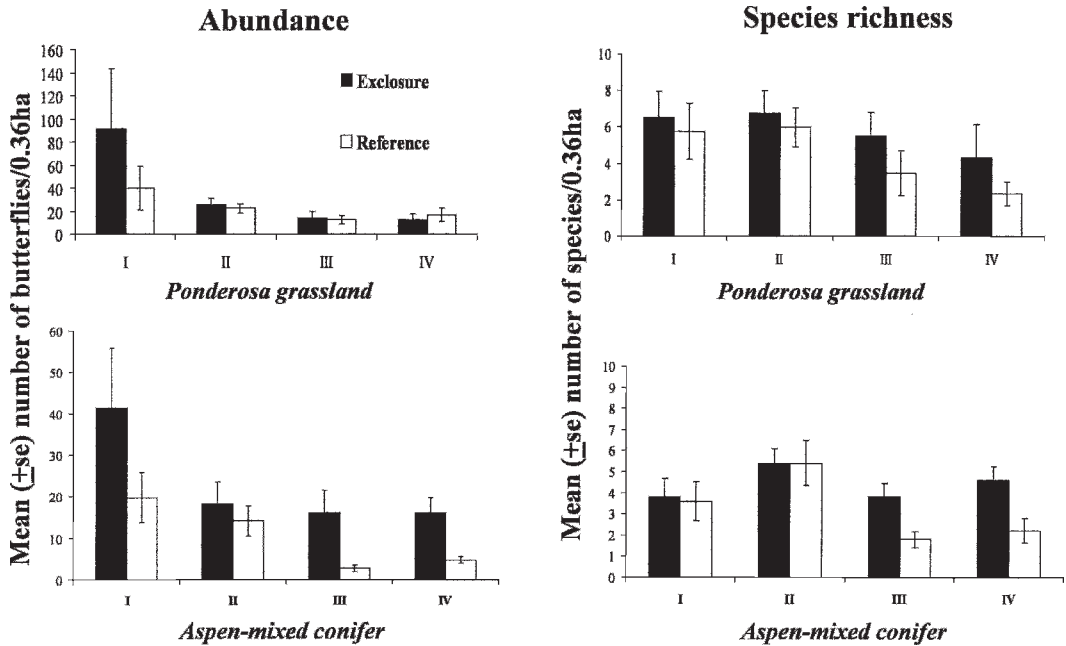


FIG. 2—Mean ($\pm$ SE) abundance and species richness of butterflies/0.36 ha observed in elk exclosure ($n = 5$) and reference sites ($n = 5$) in ponderosa pine grassland and aspen-mixed conifer forest, Bandelier National Monument, New Mexico. Sample periods in 2001 correspond to: I (1 to 10 June), II (20 June to 1 July), III (18 to 24 July), and IV (2 to 12 August).

presence of large numbers of generalist species in both habitats (*Colias eurytheme*, *Pontia protodice*, and *V. cardui*), we also used a 2-way ANOVA to compare the pooled mean butterfly abundance/summer among treatments (exclosure vs. reference), habitat types (PG vs. MC), and their interaction to test whether such ubiquitous species might be sensitive to the treatment effects. Although their mean abundances were greater in exclosed vs. reference sites, there were no significant differences between types ($F_{1,1} = 2.74$, $P > 0.05$), treatments ($F_{1,1} = 1.98$, $P > 0.05$), or their interaction ($F_{1,1} = 0.037$, $P > 0.05$) due to the high variance among sites. Butterfly species richness was positively correlated with butterfly abundance across all sampling periods in the aspen-mixed conifer ($r^2 = 0.29$, $F_{1,38} = 17.17$, $P < 0.001$), but not ponderosa pine sites ($r^2 = 0.06$, $F_{1,28} = 2.77$, $P > 0.05$).

Butterfly abundance in MC sites in 2001 was the only variable to have a significant treatment and date*treatment interaction, which was likely due to the greater number of butterflies and species observed in the exclosed aspen-mixed conifer sites during the last 2 sampling periods (III and IV), mid to late summer (Fig. 2,

Table 1). This was due to the predominance of species such as *Speyeria cybele*, *S. hesperis*, *S. mormonia*, *Cercyonis oetus*, and *Plebeius icarioides*. We define these as “late summer species” because their first or second brood adults emerge in mid to late July, when the mid-summer rains (monsoons) arrive in north-central New Mexico. A significant relationship existed between the abundance of these 5 species and forb species richness ($r^2 = 0.65$, $F_{1,19} = 17.79$, $P < 0.05$) as well as between overall butterfly species richness and forb species richness ($r^2 = 0.61$, $F_{1,19} = 15.2$, $P < 0.05$) for the same sampling periods.

When *V. cardui* were excluded from the 2001 MC analyses, richness and abundance still significantly differed ($P \leq 0.05$) for both date and treatment, but not the interaction of date*treatment. This was not surprising, because the greatest numbers of *V. cardui* were observed during the first sampling period.

Effects of Ungulate Exclusion on Vegetation—We found no significant difference in the proportions of vegetation cover types (e.g., forb, grass, tree) between exclosed and reference sites in ponderosa pine and aspen-mixed conifer sites in

TABLE 1—Results of 2-way repeated measures ANOVAs to test for the effect of date, treatment (exclosures), and date*treatment on butterfly abundance or species richness in each habitat for each year in ponderosa pine (*Pinus ponderosa*) grassland sites and in aspen (*Populus tremuloides*) and mixed-conifer forest sites at Bandelier National Monument, New Mexico. All data were log transformed before analyses, and data not meeting assumptions of ANOVA were analyzed with a Wilcoxon Signed Rank test (*) for date and treatment. Significance assessed at $P < 0.05$.

	Butterfly abundance						Butterfly richness					
	Date			Treatment			Date			Treatment		
	F or Z*			F or Z*			F or Z*			F or Z*		
	P			P			P			P		
Grassland												
1999	0.05	0.82		1.61	0.25		0.26			0.95	0.24	
2000*	-2.22	0.02		-7.75	0.43		—			0.02	0.08	
2001	3.58	0.01		1.92	0.67		0.87			0.01	0.14	
Forest												
1999	6.90	0.03		0.03	0.85		0.27			0.04	0.92	
2000*	-1.70	0.08		-1.57	0.11		—			0.17	0.27	
2001	17.35	<0.01		4.89	0.05		0.02			0.01	0.02	
2001 ^a	4.22	0.02		5.35	0.05		0.37			<0.01	0.05	
2002	1.94	0.13		1.80	0.21		0.89			0.16	0.26	

^a Analysis omitting butterfly *Vanessa cardui*.

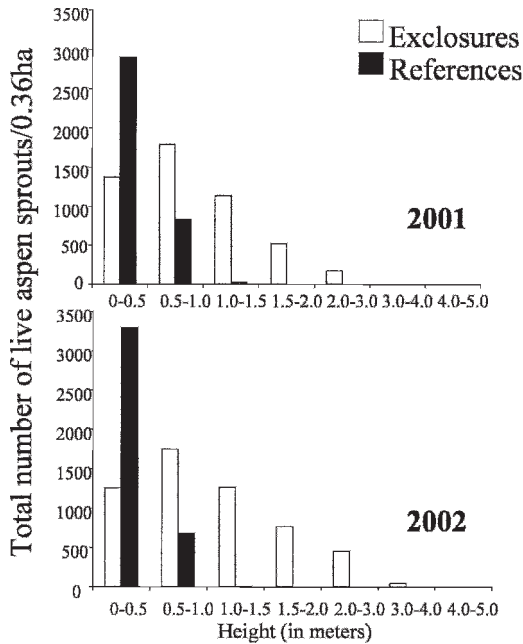


FIG. 3.—Abundance of live aspen sprouts in each height stratum (0 to 5.0 m) within aspen-mixed conifer forest exclusion and reference study areas, August 2001 and 2002, at Bandelier National Monument, New Mexico. There was a significant difference in the distribution of stems within both years (2001: $\chi^2 = 2527.9$, $df = 4$, $P < 0.001$; 2002: $\chi^2 = 3724.6$, $df = 4$, $P < 0.001$).

1999 and 2000 (all t -tests $P > 0.05$). Mean frequency of the most abundant blooming forbs also did not differ between treatments in 2001 in either habitat type (all paired t -tests $P > 0.05$). In aspen-mixed conifer sites, neither forb nor grass biomass significantly differed between treatments within 2001 or 2002. However, mean ($\pm$ SE) non-woody biomass was significantly greater in 2001 compared to 2002 in both the exclusions (17 ± 4.79 SE vs. 2.68 ± 1.13 SE, $t = 3.77$, $df = 4$, $P < 0.05$) and the reference areas (14.06 ± 3.91 SE vs. 1.67 ± 0.48 SE, $t = 3.51$, $df = 4$, $P < 0.05$). Height distributions (6 strata between 0 and 4.0 m) of live understory aspen stems significantly differed between excluded and reference sites in 2001 ($\chi^2 = 2527.9$, $df = 4$, $P < 0.001$) and 2002 ($\chi^2 = 3724.65$, $df = 4$, $P < 0.001$) (Fig. 3).

Butterfly Community Structure—The NMS ordination showed a clear separation of the “late summer” butterfly species community occupying sites excluded from elk compared to those observed in the reference areas (Fig. 4). The

proportion of variation explained by axis 1 was 57%, with an additional 19% explained by axis 2, for a cumulative coefficient of determination of $r^2 = 0.76$. Measured stress of real data was equal to the minimum of the Monte Carlo simulation (Ax1: $P < 0.05$, Ax2: $P < 0.05$), so confidence was lower than desired, yet stability was good.

Given the placement and length of the vectors (representing environmental variables) along the axes, the ordination suggested that the species community composition of butterflies in sites excluded from elk was influenced by a greater abundance of non-woody biomass (*GRASSgm*, *FORBgm*), forb richness (*BLOOMspp*), frequency of blooming forbs (*BLOOMfreq*), and regenerating aspen 0.05 to 1.50 m in height (*ASPEN#*) in the excluded sites. Only one exclusion site, MC3 during sampling period III, was an anomaly to the observed pattern. This was because only 2 butterflies (*V. cardui* and *S. hesperis*) were observed in the site, as was the same for MC5ref during period IV. In general, fewer butterflies were observed in the reference areas, and only one butterfly was observed in each of the excluded outlier sites; MC4ref and MC5ref, period III. The ordination clearly demonstrated a strong relationship between the unexcluded reference sites and an abundance of “browsed” aspen stems (0.01 to 0.49 m).

DISCUSSION—Our exclusion experiment suggests that lack of browsing by high numbers of elk in the western mountains can have a variable and indirect affect on butterfly community structure due to changes in vegetation structure and composition. This supports the variable results found by others investigating the impact of wild ungulate herbivory upon arthropod species richness and abundance (Baines et al., 1994; Pollard and Cooke, 1994; Rambo and Faeth, 1999; Feber et al., 2001; Bailey and Whitham 2002).

Although elk were only excluded for 4 y, our results indicated that, at high densities, elk can reduce “growing season” non-woody biomass, forb richness, and aspen regeneration and, therefore, potentially alter adult butterfly species community composition in aspen-mixed conifer forests. It seems, however, that elk have little or no impact on summer vegetation or butterflies in lower-elevation ponderosa pine grasslands of the Jemez Mountains. In support of these findings, dietary analyses, radiotelemetry, and observa-

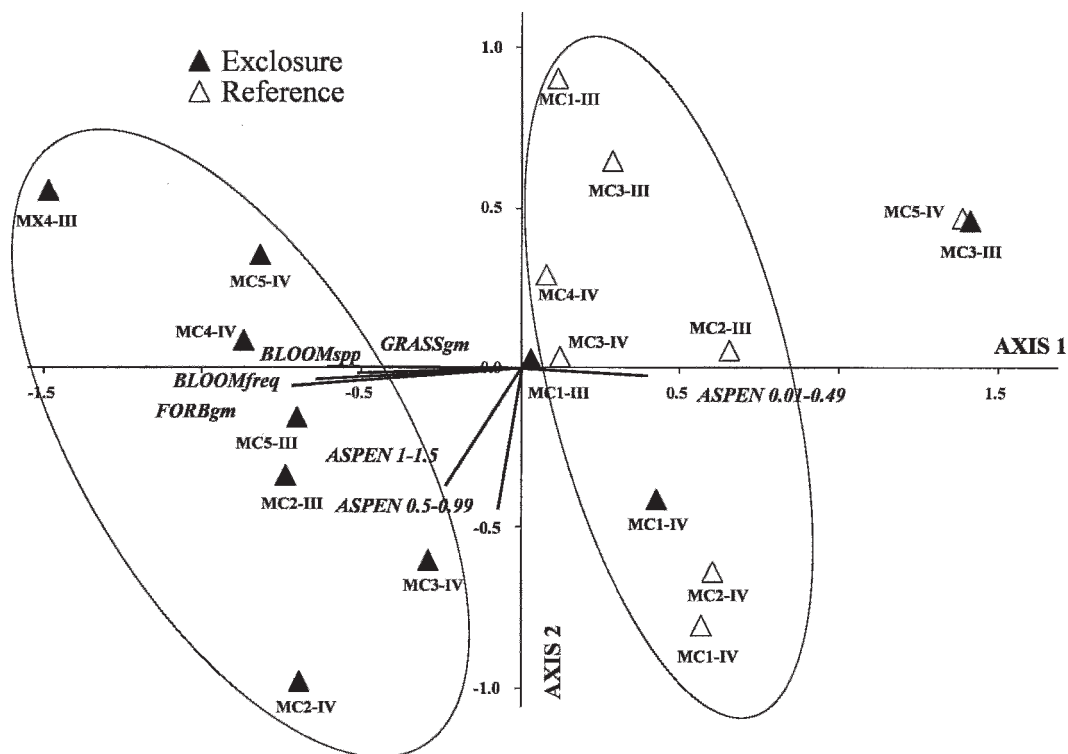


FIG. 4—Nonmetric Multidimensional Scaling (NMS) ordination of the butterfly species composition of enclosure (▲) and reference (△) sites at Bandelier National Monument, New Mexico, during late summer (18 July through 12 August 2001) sampling periods III and IV ($n = 18$). Length and direction of vectors represent the environmental variables most correlated with the axes of those tested: forb biomass, grass biomass, blooming forb frequency, blooming *Potentilla* frequency, blooming forb richness, and live aspen stem density in the height strata of 0.01–0.49, 0.50–0.99, and 1.00–1.49 m. Proportion of variation explained by Axis 1 was 0.57 and by Axis 2 was 0.19, for a cumulative coefficient of determination of $r^2 = 0.76$.

tions of fresh pellets and grazing and bedding sites in Bandelier NM indicate that elk migrate to higher elevations in spring and use aspen-mixed conifer forests and mountain meadows throughout the summer (Wolters, 1996; Fettig, unpublished data). Moreover, aerial surveys of radio-collared elk indicate that elk spend the majority of winter below 2,700 m on mesas in the region, which are primarily comprised of ponderosa pine grasslands. Any herbivory and trampling that occurs is prior to the growing season and, therefore, would have little measurable impact on butterflies and their larval and nectar hostplants.

We observed more butterflies in 2001 than we did in any other year. Not only were there large numbers of generalist species, but we also observed greater species richness. Both habitats had significantly greater counts of butterflies

early in the summer of 2001 due to the presence of *V. cardui*. On several occasions in June, we counted 50 to 100 *V. cardui* per bush of *Ceanothus fendleri* in the ponderosa pine grasslands, which accounted for large deviations from our mean total number of butterflies. Compared to the past 30 y, the winter of 2000 to 2001 received average precipitation. This most likely provided ample moisture for development of larval hostplants and butterflies in comparison to 1999 to 2000 and 2001 to 2002, which had lower than normal precipitation, resulting in drought-like conditions each subsequent spring (Fenton, unpublished data). We also attributed the greater amount of non-woody biomass and abundance of blooming forbs in the aspen-mixed conifer sites in 2001 to this moisture.

Results of regression and ordination analyses indicated that butterfly abundance, richness, and

species community composition in the aspen-mixed conifer sites were positively and significantly associated with forb biomass and richness. We also found that individual sites with the greatest forb biomass supported the most butterflies. This supports the inference of Rambo and Faeth (1999) that insect abundance increases in ungrazed vegetation due to the availability of greater biomass or structural complexity. In our study area, greater forb biomass and richness of blooming forbs might have provided adult butterflies with a greater abundance and diversity of nectar sources and oviposition sites. We speculate that an increase in habitat complexity might be important for the "late season" flying butterflies. Grazing and trampling by elk potentially reduce biomass and plant height as it increases over the growing season. Thus, we hypothesize that lack of any treatment effects during the early summer sampling periods might have been due to lack of biomass accumulation, especially in those years having lower winter and spring precipitation. We also attribute the lack of significant differences between treatments for individual environmental variables (e.g., percent of vegetation cover types, forb richness, frequency of blooming forbs, non-woody biomass) in either habitat, because 3 y of elk exclusion was not enough time to observe measurable changes in vegetation, if present, or that effects of drought might have overwhelmed the otherwise gradual development of differences between treatments.

The ordination analysis of species community composition was helpful for interpreting detectable differences between treatments in the aspen-mixed conifer forest sites in 2001. The placement of the majority of enclosure and reference sites in ordination space were clearly separated from each other along Axis 1, representing greater forb availability at one extreme. For example, MC4ex and MC5ex were most associated with greater forb and grass biomass, forb richness, and frequency of blooming forbs. Both sites had well-developed understory vegetation, and MC4ex had patches of open meadow containing a variety of forbs. It also contained a patch of the woody shrub *Potentilla fruticosa*. Immediately outside the enclosure, *P. fruticosa* was heavily browsed by elk and produced no flowers, and we quantified butterflies nectaring on *P. fruticosa*, *P. pulcherrima*, and *P. hippiana* (unpublished data). All of these *Potentilla* species

are browsed by elk in the Jemez Mountains or other regions of the Rocky Mountains (Kufeld, 1973; Rowland et al., 1983; Wolters, 1996; Rambo and Faeth, 1999). Further study of the importance of this genus for butterflies might provide important clues as to the effects of elk herbivory upon nectar availability for adult butterflies within our study area.

The reference sites were spaced more closely together along Axis 1 and were most associated with a greater number of aspen sprouts (<0.49 m) outside the enclosures as a result of height suppression and resprouting from overbrowsing. Likewise, the enclosures contained more aspen stems (0.5 to 1.5 m). This was also evident in the significant differences among height strata of aspen stems between treatments. Lack of stems (>2.0 m) indicated that the enclosures allowed aspen regeneration and that the high numbers of elk in the region were limiting aspen regeneration, similar to that reported for other areas of the Rocky Mountains (Sheppard and Fairweather, 1994; Romme et al., 1995; Baker et al., 1997; Kay, 1997; White et al., 1998; Ripple and Larsen, 2000; Kay, 2001; Ripple et al., 2001).

We attribute the spread and variability among enclosure sites along both axes to their variable response to the absence of elk and to the presence of fire. Historically, a 10-year to 15-year fire regime occurred in the aspen-mixed conifer forests of the Jemez Mountains (Allen, 1989). Such fires would have maintained a greater percentage of aspen stands and would have facilitated growth of understory vegetation. Fortunately, 2 of our sites (MC2ex and MC2ref) were burned in the May 2000 Cerro Grande Fire. MC2ex was one of the sites that contained a high number of aspen stems and high number of butterflies, although mostly habitat generalists. As suggested by the ordination, we suspect that the burn accounted for the stronger correlation of regenerating aspen, browsed (<0.49 m) and unbrowsed (0.5 to 1.5 m), with the community composition of butterflies on the MC2ref or MC2ex sites.

Bailey and Whitham (2002) found arthropod abundance and species richness to be larger in areas of greater aspen regeneration as a result of high burn severity and absence of elk. We found a similar pattern for butterflies, although a clear explanation for the greater numbers of butterflies in areas of greater aspen regeneration

remains unknown and warrants continued study. We speculate, however, that the early successional habitat allowed for greater light penetration, reflectivity and warmer temperatures conducive to forb growth, i.e., more biomass for greater larval hostplant and adult nectar plant availability (Feber et al., 2001). In addition, the sunlight and structure might have provided more basking, mate-searching, and oviposition sites or protection from birds, although these behaviors do not necessarily occur in the same location (Gilbert and Singer, 1973). Because some species of butterflies are known to inhabit early successional openings in woodlands, the preexisting meadows and the regenerating aspen within our study sites provided habitat in an otherwise dense aspen-mixed conifer forest (Feber et al., 2001).

If corroborated by continued monitoring, results of our enclosure experiment provide further evidence that high numbers of elk can suppress aspen regeneration and also alter understory non-woody vegetation in the southern Rocky Mountains, and that another herbivore (i.e., butterflies) might be responding to this change in some locations in some years. Although questions remain as to the exact mechanisms and synergistic effects of how such alterations in plant structure and community composition influence butterfly numbers and richness, our data suggest that if browsing by ungulates is to have an effect upon butterflies, it is primarily those with a mid-to-late summer flight period in the aspen-mixed conifer forest. Additional work is needed to determine if this is a short-term phenomenon or holds for other seral stages and habitats. Similarly, we question whether the relation between butterflies and forbs will change with community succession. Although limited, our data suggest that a trophic cascade might extend from elk and vegetation to butterflies.

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APPENDIX—Abundance of each butterfly species observed on ungulate exclosure (Exc) and Reference (Ref) Areas in ponderosa pine (*Pinus ponderosa*) grassland sites and in aspen (*Populus tremuloides*) and mixed-conifer forest sites at Bandelier National Monument, New Mexico, 1999 through 2001. Sampling periods 2–4x varied among years.

[illegible]

APPENDIX—Continued.

	Grassland sites (n = 4)						Forest sites (n = 5)					
	1999		2000		2001		1999		2000		2001	
	Exc	Ref	Exc	Ref	Exc	Ref	Exc	Ref	Exc	Ref	Exc	Ref
Mourning Cloak, <i>Nymphalis antiopa</i>	—	—	—	—	—	—	—	—	—	—	—	5
American Lady, <i>Vanessa virginiensis</i>	—	—	—	—	—	—	—	—	—	—	5	1
Painted Lady, <i>V. cardui</i>	—	—	—	—	326	142	—	—	4	—	177	99
Red Admiral, <i>V. atalanta</i>	—	—	—	—	—	—	1	2	—	—	—	1
Subfamily Limenitidinae												
Weidemeyer's Admiral, <i>Limenitis weidemeyerii</i>	—	—	—	—	—	—	—	—	—	—	1	—
California Sister, <i>Adelpha bredowii</i>	1	—	—	—	1	1	—	1	—	—	—	—
Subfamily Satyrinae												
Small Wood-nymph, <i>Cercyonis oetus</i>	—	—	—	—	—	—	—	—	8	—	35	7
Subfamily Danainae												
Monarch, <i>Danaus plexippus</i>	—	—	—	—	5	—	—	—	—	—	1	—
Family Hesperidae (species pooled)*	—	—	3	5	5	4	—	—	9	—	27	13
Species richness (excluding Hesperidae)	10	10	5	4	16	13	5	6	6	4	17	13
Total number of butterflies	100	59	10	10	562	339	10	11	46	11	456	208

* Silver-spotted Skipper, *Epagyreus clarus*; Northern Cloudywing, *Thorybes pylades*; Mexican Cloudywing, *Thorybes mexicana*; Rocky Mountain Duskywing, *Erynnis telemachus*; Pacuvius Duskywing, *Erynnis pacuvius*; Common Checkered-Skipper, *Pyrgus communis*; Draco Skipper, *Polites draco*; Tawny-edged Skipper, *Polites themistocles*; Taxiles Skipper, *Poanes taxiles*; Orange-headed Roadside-Skipper, *Amblyscirtes phylace*.