Journal of Arid Environments 72 (2008) 904–913

Journal of Arid Environments

www.elsevier.com/locate/jaridenv

Do ungulates facilitate native and exotic plant spread? Seed dispersal by cattle, elk and deer in northeastern Oregon

Anne M. Bartuszevige[a,*], Bryan A. Endress[b,1]

[a]Eastern Oregon Agricultural Research Center and Department of Fisheries and Wildlife, Oregon State University, P.O. Box E, Union, OR 97883, USA

[b]Department of Forest Science, Forestry and Range Sciences Laboratory, Oregon State University, La Grande, OR 97850, USA

Received 26 June 2007; received in revised form 19 November 2007; accepted 22 November 2007
Available online 4 January 2008

Abstract

Large domestic and native ungulates have the potential to disperse large quantities of seeds throughout the landscape. Many studies have found that ungulates are capable of dispersing seeds but few quantify the relative importance of ungulate dispersal across the landscape. We investigated the potential for cattle, elk, and deer to disperse native and exotic plants in two different western North American ecosystems in northeast Oregon. We collected fecal samples of cattle, elk and deer that had been deposited during the current growing season. In the greenhouse we monitored the density and species richness of seedlings that germinated from the fecal samples. All three species act as seed dispersers for native and exotic plants. Cattle fecal pats had a higher species richness and density of exotic grasses germinating compared to the other ungulates; elk had a higher species richness and density of native and exotic forbs compared to the other ungulates. We then projected the number of seeds that each animal could disperse during a growing season. We predict that cattle disperse more than an order of magnitude more seeds than elk and deer per animal. Cattle, elk and deer interact with the landscape in different ways and this can have important ramifications for plant communities at local and regional scales.

Keywords: *Bos taurus*; *Cervus elaphus*; Grasslands; Invasive plants; Coniferous forest; *Odocoileus* sp.; Rangeland

1. Introduction

Janzen (1984) hypothesized that the seeds of many plant species used as forage by ungulates may, in fact, be adapted for dispersal via the guts of ungulate herbivores. Since that time, most research on the topic of seed dispersal has concentrated on fruit and their frugivore consumers and seed dispersers; however, some investigators have pursued this hypothesis. Of the few ecological studies that have studied seed dispersal by ungulates, most have occurred in the old world (Cosyns et al., 2005a, b; Couvreur et al., 2005; Gardener et al., 1993; Malo et al., 2000; Milton and Dean, 2001; Radford et al., 2001; Ramos et al., 2006; Traba et al., 2003).

*Corresponding author. Tel.: +1 541 562 5129; fax: +1 541 562 4358.
E-mail addresses: anne.bartuszevige@oregonstate.edu (A.M. Bartuszevige), bendress@sandiegozoo.org (B.A. Endress).
[1]Current address: Conservation and Research for Endangered Species, Zoological Society of San Diego, 15600 San Pasqual Valley Road, Escondido, CA 92027, USA.

0140-1963/$ - see front matter
doi:10.1016/j.jaridenv.2007.11.007

However, only a few of these studies have compared the relative importance of endozoochorous seed dispersal by native and domestic ungulate species (Cosyns et al., 2005a; Malo et al., 2000; Milton and Dean, 2001). In North America, many studies of seed dispersal by ungulates have focused primarily on the potential for livestock to disperse seeds of exotic species (Carpinelli et al., 2005; Doucette et al., 2001; Fredrickson et al., 1997; but see Ocumpaugh et al., 1996; Olson et al., 1997). In these studies, seeds of the focal exotic plant are fed to livestock (usually cattle (*Bos taurus*) or sheep (*Ovis aries*)) and the feces collected. An alternative method used is to place the seeds in the rumen for a designated period of time. After collection, the fecal or rumen material is washed from the seeds and the seeds germinated in a greenhouse. The information gained from these studies addresses whether livestock are capable of passing viable seeds, but does not provide information about whether livestock represent a significant dispersal mechanism across the landscape.

Information about the importance of native ungulates as seed dispersers in the United States is also rare (Ford et al., 2003; Myers et al., 2004; Vellend, 2002; Vellend et al., 2003; Vilà and D'Antonio, 1998; Wald et al., 2005). Myers et al. (2004) found that white-tailed deer (*Odocoileus virginianus*) were important dispersers of understory annual and perennial herbs in the eastern deciduous forest. Furthermore, both Myers et al. (2004) and Vellend (2002) documented that white-tailed deer were capable of dispersing seeds of invasive, exotic species. Vellend et al. (2003) concluded that white-tailed deer could be responsible for long-distance dispersal of understory herbs.

While ecologists have long-recognized the importance of animal-mediated seed dispersal, it remains unclear how important endozoochory is in initiating or increasing invasive plant infestations in natural systems (Gill and Beardall, 2001). Endozoochorous seed dispersal by white-tailed deer in eastern North America may play a considerable role in invasive plant spread; 64% of species and 95% of all viable seeds in deer pellets may be of non-native origin (Myers et al., 2004). Beyond this study, we are aware of no other comprehensive multi-species studies that have examined the importance of endozoochory by ungulates for invasive plant spread. Consequently, we know surprisingly little about the role ungulates play in plant invasions and plant community dynamics in the ecosystems of western North America. This is particularly surprising because native and introduce ungulates dominate most western US landscapes. Viable seeds of invasive plants have been recovered from dung in several studies, but data are limited to a small handful of species including leafy spurge (*Euphorbia esula*), common crupina (*Crupina vulgaris*), spotted knapweed (*Centaurea maculosa*), and Lehmann lovegrass (*Eragrostis lehmanniana*) (Fredrickson et al., 1997; Olson et al., 1997; Wallander et al., 1995).

In this study, we examined the relative contributions of three ungulates to seed dispersal. The purpose of this study was to determine which native and exotic plant species are dispersed by cattle, elk (*Cervus elaphus*) and deer (*Odocoileus* sp.) in northeastern Oregon and evaluate the relative importance of the different ungulates to the dispersal of native and exotic species across the landscape.

2. Materials and methods

2.1. Study areas

Research was conducted at Zumwalt Prairie Preserve and Starkey Experimental Forest and Range, both in northeastern Oregon, USA. Both ecosystems were representative of rangeland types in the interior northwestern United States.

The Zumwalt Prairie (45°31′N, 117°3′W; hereafter referred to as Zumwalt) was the last large (approximately 65,000 ha) remnant of native northwest bunchgrass prairie. Due to its higher elevation, the Zumwalt was colder and drier than other regions of northwest bunchgrass prairie. For this reason, and due to its isolation, the Zumwalt remained relatively intact and was dominated by bunchgrasses, especially Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoregnaria spicata*) and Sandberg's bluegrass (*Poa secunda*) with a high diversity of forbs. Very little of the prairie was cultivated (Bartuszevige and Kennedy, unpublished data) and the current primary landuse is spring/summer cattle production. In 2001, The Nature Conservancy (TNC) purchased a portion of the Zumwalt Prairie (4946 ha), creating their Zumwalt Prairie Preserve. Approximately, 320 native and 80 exotic plant species were found on the preserve. We collected fecal samples on the TNC preserve.

The 10,000-ha Starkey Experimental Forest and Range (45°13′N, 118°31′W; hereafter referred to as Starkey) has been the site of long-term studies of cattle, mule deer, and elk during the past 40 years (Rowland et al., 1997; Skovlin, 1991), and was associated with an intensive database on ungulate-environment relations (Rowland et al., 1998, 2000). Elevations at Starkey vary from 1122 to 1500 m. Precipitation averaged about 500 mm/year, almost all of which comes in the fall as rain or snow in the winter. Temperatures ranged from −4 °C in the winter to 31 °C in the summer. Approximately, 70% of Starkey was covered by coniferous forests (ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*, and mixed conifer stands), and the remaining 30% perennial bunchgrass grasslands and meadows dominated by Idaho fescue, bluebunch wheatgrass, and Sandberg's bluegrass.

2.2. Fecal sample collection and seed germination

Between July and September 2005, we collected fecal samples from cattle (one sampled collected in July, seven in August, three in September), elk (10 samples each in July and August) and deer (two samples in July and eight in August) that were recently deposited in our two study areas. Both mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) are found at Zumwalt and Starkey. Although mule deer are much more abundant than white-tailed deer in northeastern Oregon, we were unable to determine to which species the fecal sample belonged; therefore, these samples were labeled generally as "deer". We defined "recently deposited" as fecal samples that were defecated during the 2005 grazing season (May–September); samples were dark brown to black in color and had not been bleached by the sun. We collected 10 fecal samples from each ungulate species at each field site except for deer which we collected eight samples from Starkey and two samples from Zumwalt. We placed fecal samples into individual paper bags, labeled and stored them at 5 °C until they were planted in the greenhouse. The size of fecal samples ranged considerably among ungulates, and cattle deposited the largest fecal units ($1053\,cm^3 \pm 180.4$ S.E.), followed by elk ($240\,cm^3 \pm 26.7$ S.E.), and deer ($70\,cm^3 \pm 22.9$ S.E.). Because of the large size of the cattle pats, only a portion of each unit (approximately one-third) was used for the germination trials.

In the greenhouse, we placed individual unbroken fecal samples in 11.4 L plastic pots filled with commercially available organic potting mix. We placed an additional five pots with the potting mix but no fecal material in the greenhouse to detect possible contamination from the soil medium or the greenhouse. We maintained the greenhouse at ambient light and humidity and at typical early summer temperatures for northeast Oregon (27/19 °C d/n). We watered the pots as needed and rearranged them on the bench randomly every week. As seedlings emerged, we identified (Hitchcock and Cronquist, 1973), counted, and removed seedlings. We classified seedlings by origin (native or exotic) and growth form (graminoid, forb, shrub, or tree). After 3 months or all seedlings in a pot were identified, whichever came last, we gently broke the feces apart to stimulate additional germination. After additional 3 months or when all seedlings in a pot were identified, whichever came last, we ended the study for that pot.

2.3. Data analysis

We performed a two-way analysis of variance (Proc GLM) in SAS (SAS Institute, 2002) to test for differences in the mean number of germinating seeds/100 cm^3 of feces (an estimate of seed density) among ungulates and sites. We assessed differences among the three ungulates in the proportion of germinable seeds belonging to five plant functional groups (native forb, exotic forb, native graminoid, exotic graminoid, native shrub) using a log-likelihood goodness-of-fit test. Due to the low number of deer fecal samples ($n = 8$ at Starkey and $n = 2$ for Zumwalt) and the low number of germinated seeds in deer feces (21 seeds), only cattle and elk were included in the analysis of variance analysis.

2.4. Estimating seed rain across the landscape

Data from our seed germination samples were then integrated with data on ungulate densities and defecation rates to estimate the number of native and exotic seeds potentially dispersed by cattle, elk, and deer across the Wallowa-Whitman National Forest. Ungulate density estimates came from 1998, 2000 and 2001 ungulate population census data and grazing statistics for the Wallowa-Whitman National Forest (Schommer and Johnson, 2003; Wallowa Whitman National Forest, 2001). These records indicate that approximately 80,570 ungulates are found throughout the National Forest, with summer densities of 3.13 cattle/km^2, 2.03 mule deer/km^2, and 1.46 elk/km^2. Defecation rates for cattle have been estimated at approximately 12 defecation events per day (Dwyer, 1961; Wagnon, 1963). Defecation rates for deer are estimated at 35 pellet groups per day (Rogers, 1987) and we assumed defecation rates for elk to be the same rate as cattle. We then estimated the number of germinable seeds potentially dispersed by each ungulate over a 3-month season (June–August) per km^2 assuming a uniform distribution using the following equation:

$$\text{Ungulate density (per km}^2) \\ \times \text{ median number of germinable seeds per fecal unit} \\ \times \text{ daily defecation rate} \times 90 \text{ days.}$$

3. Results

Fifty-two different species of plant seeds germinated in 43 of 50 fecal samples collected (Table 1) and no plants were discovered in the five pots in which no fecal samples were placed. A total of 878 seeds germinated in the fecal samples that we have collected, 434 germinated from fecal samples collected from Starkey and 444 germinated from fecal samples collected from Zumwalt (Table 1). Cattle feces had the largest number of germinating seeds and deer had the smallest number of germinating seeds (Table 1). Of the 52 species identified, 42 were found in cow fecal samples, 27 species in elk fecal samples, and 11 species were found in deer fecal samples. A complete list of species identified is in the Appendix.

The mean density of germinating seeds/100 cm^3 of fecal material did not differ among cattle and elk ($F = 1.38$, $p = 0.66$). On average, cattle feces contained 8.0 ± 1.7 S.E. germinable seeds/100 cm^3, followed by elk (5.0 ± 1.6 S.E. germinable seeds/100 cm^3), and deer (5.0 ± 2.0 S.E. germinable seeds/100 cm^3). However, differences were found in the type of germinating seeds in cattle and elk feces ($G^2 = 81.93$, d.f. = 2, $p < 0.0001$; Fig. 1). Elk feces contained over twice as many native seeds as cattle (41% vs. 20%). Over 70% of germinable seeds in cattle feces were exotic grass species (e.g. *Poa pratensis*), compared to just 34% of germinable seeds in

Table 1
Germinable seeds in cattle, elk, and deer feces collected at two sites in northeastern Oregon in 2005

	Starkey experimental forest			Zumwalt prairie preserve		
	Cattle ($N = 10$)	Elk ($N = 10$)	Deer ($N = 8$)	Cattle ($N = 10$)	Elk ($N = 10$)	Deer ($N = 2$)
Percentage of samples with germinable seeds	100	70	63	100	90	100
Number of germinated seeds	333	90	11	280	154	10
Seed density (germinations/100 cm^3 feces)						
Median	5	1	1	9	5	6
Maximum	29	16	8	19	28	9
Species richness per fecal sample						
Median	5	4	1	6	1	4
Maximum	25	11	5	14	8	5
Percent contribution by functional group						
Native graminoid	3.7	13.6	62.8	7.6	4.0	10.8
Exotic graminoid	55.3	10.9	15.7	73.8	46.5	27.0
Native forb	23.6	49.2	13.7	10.0	20.6	21.6
Exotic forb	17.4	23.2	7.8	8.6	28.9	40.5
Native shrub	0	3.2	0	0	0	0
Total number of germinating species	25	21	7	28	13	3
Percent of total germinated seeds	38	10	1	32	18	1

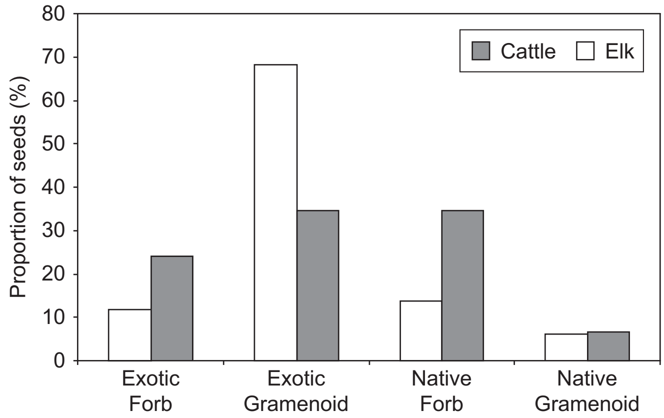

Fig. 1. Percent of seeds of five different life forms found germinating in cattle and elk feces. Starkey and Zumwalt sites were pooled since no differences were found in seed germination rates among the sites.

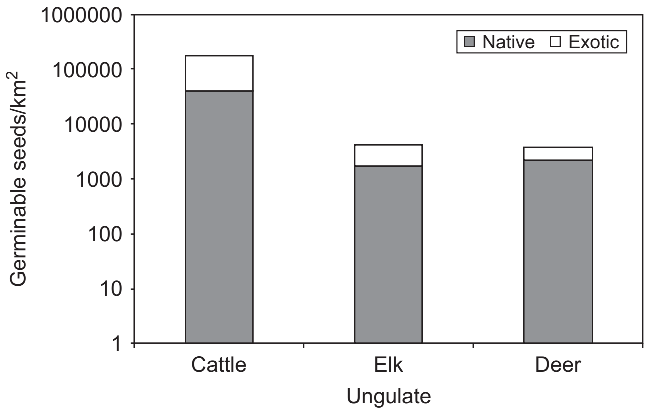

Fig. 2. Estimated number of germinable native and non-native seeds dispersed by endozoochory/km^2/year in the Wallowa-Whitman National Forest, in northeastern Oregon. Note the log scale on the *y*-axis.

elk feces. No differences were found in the mean density of seed germinating between the two sites, and no interactions were found.

Due to high density of cattle across the landscape and the large size of fecal deposits, we predict that cattle can disperse more germinable seeds than native ungulates (Fig. 2). Cattle are projected to disperse over 1.78 million seeds/km^2 in the Wallowa-Whitman National Forest every growing season. Since approximately 70% of germinable seeds found in cattle feces are exotic, this corresponds to approximately 1.2 million-germinable exotic seeds/km^2. This is two orders of magnitude greater than our projections for elk and deer for the same area (Fig. 2). At the same time, due to the large numbers of germinable seeds potentially dispersed by cattle, cattle are also the primary dispersers of native seeds, dispersing approximately 39,700 germinable native seeds/km^2 as compared to elk (1680 germinable native seeds/km^2) and deer (2122 germinable native seeds/km^2).

4. Discussion and conclusions

Seeds germinated from feces of cattle, elk and deer; cattle fecal material had the most germinating seeds. Other researchers have investigated the potential for cattle to disperse seeds (Carpinelli et al., 2005; Cosyns et al., 2005a, b; Doucette et al., 2001; Gardener et al., 1993; Ocumpaugh et al., 1996; Radford et al., 2001;

Traba et al., 2003); however, few studies have investigated the ability of native ungulates (elk and deer) to disperse viable seeds (Malo and Suárez, 1998; Malo et al., 2000; Milton and Dean, 2001; Myers et al., 2004; Vellend, 2002). We projected that native ungulates are also capable of dispersing large quantities of seeds (Fig. 1).

A disproportionate number of exotic species germinated from cattle fecal pats and most of those species were exotic grasses. We do not have data regarding cattle preference for native or exotic grasses. Therefore, we are unable to draw conclusions about whether more exotic species are found in cattle fecal pats because (1) they are a preferred forage, (2) the native seeds are more easily digested in the rumen of the cattle compared to exotic seeds, (3) exotic species have higher fecundity and therefore more seeds available for consumption, or (4) exotic seeds are smaller and less likely to be damaged in the rumen. More investigation into cattle forage preference for exotic species in grassland and forest ecosystems and the resulting effects on seed viability and dispersal is needed.

Elk had a higher proportion of forbs germinating from their feces than cattle and were the only species to have shrub species germinate. This is likely due to elk diet: local diet analyses indicate that elk prefer forbs and shrubs to grass species (Wisdom, 2005). Elk also had a greater proportion of exotic forb species germinate from their feces than cattle. This also may be due to their diet preference for forb species. Thus, elk likely play a role in dispersing exotic species across the landscape; however, their role in dispersing exotic species is tiny compared to cattle because of their lower densities and lower consumption rates (and thus defecation rates). As a result, despite the greater proportion of exotic seeds germinating from elk, cattle were projected to disperse over 20 times as many germinable exotic forb seeds/km^2/year than elk.

Due to low densities and small size of fecal units, deer disperse a very low amount of germinable seeds across the landscape. We had low sample sizes for deer which make inference difficult. Deer may have a small enough rumen and, therefore, seeds of many different species will be viable when passed, but are more selective in their browsing than cattle or elk (Wisdom, 2005).

We projected that cattle disperse a disproportionate number of seeds, and exotic seeds in particular, in the Wallowa-Whitman National Forest compared to elk and deer (Fig. 1). Differences in movements and interspecific interactions among these species have consequences for plant community dynamics and long distance dispersal of native and exotic plants.

The distance and direction of dispersal events for exotic species by cattle on public lands is limited due to the constraints of fences that designate allotments. The number of livestock grazing in US national forests has been declining since the 1970s. However, they are the dominant ungulate on the Wallowa-Whitman National Forest (Schommer and Johnson, 2003; Wallowa Whitman National Forest, 2001), and are likely the dominant ungulate in most national forests, excluding wilderness areas. Seed dispersal by cattle on public land in the United States is likely restricted to allotment pastures. However, long-distance seed dispersal between pastures may occur when cattle are rotated (Couvreur et al., 2004). Within allotment pastures, seed dispersal may be more spatially diverse. Several studies have documented the non-random pasture use of cattle (DelCurto et al., 2005; Parsons et al., 2003; Roath and Krueger, 1982; Tate et al., 2003). Cattle use riparian areas disproportionate to their availability in the environment, particularly in the late summer (DelCurto et al., 2005; Parsons et al., 2003) when many plants have mature seeds ready for dispersal. Tate et al. (2003) found higher densities of cattle feces at cattle attractants (e.g. water points, gentle slopes). The disproportionate use of pastures near cattle attractants may mean that there is a greater density of seeds deposited there. The high levels of disturbance and increased nutrient enrichment at cattle attractants may encourage the growth of weedy or exotic plants (Brooks et al., 2006). Future research should investigate the relationship between cattle attractants and the density and cover of weedy and exotic plants.

Unlike cattle, movements by elk and deer are not constrained by allotment fences on national forests or other rangelands. Therefore, although their numbers are smaller than cattle across the landscape, they may be responsible for most long-distance dispersal events. Vellend et al. (2003) projected that white-tailed deer could disperse native *Trillium grandiflorum* seeds up to 4 km from the parent plant. Maximum elk home ranges are estimated at 1590 ha (Szmenthy et al., 1994) or 4000 m in length (Pakeman, 2001) and gut retention times are similar to deer (Barnes et al., 1992; Milne et al., 1978). So elk can potentially disperse seeds at least as far as deer are capable. Even though elk and deer are capable of dispersing seeds long distances, they are likely to deposit seeds in different habitats. Research from Starkey has demonstrated that the elk and mule deer occupy different habitats, most likely in an attempt to avoid each other (Johnson et al., 2000). In their study, elk selected for gentle slopes, areas away from roads, and westerly aspects. Mule deer selected areas to avoid elk which included steeper slopes, areas closer to roads, and easterly aspects. The differences in habitat selection and the apparent avoidance of mule deer by elk can have important consequences for seed dispersal dynamics.

Despite their lower abundance in the landscape, elk and deer can have important influences on long distance dispersal of native and exotic plant species. Vellend et al. (2003) provided hypothetical evidence that white-tailed deer contributed to long distance dispersal of forest understory herbs after the last ice age. Elk and mule deer may have similarly contributed to long distance dispersal of western plants during the same time frame. In addition, both species defecate viable seeds of exotic plants, and they may contribute to the spread and invasiveness of some exotic species.

We have shown that native and domestic ungulates in western North American ecosystems are capable of dispersing large quantities of native and exotic seeds. We germinated seeds in fecal pats in the greenhouse, where conditions were ideal for germination. Ideally, fecal pats should be monitored *in situ* to determine the number of seeds that will germinate. In addition, we did not control the diet of the animals and therefore cannot make inferences about the probability of exotic or native species being passed in a viable condition. Finally, we collected fecal pats only during the summer months at the height of seed production for many plants; however, more seeds may be dispersed earlier and later in the season. Future research should address diet preference in cattle and elk in regards to native vs. exotic species and the probability of passing viable seeds of each type.

Acknowledgments

We would like to thank the field crew members who assisted in collecting fecal samples and maintaining the greenhouse. Daahlkhaijav Damiran, Enkhjargal Darambazar, and Susan Geer assisted with seedling identification. The Nature Conservancy allowed access to their property and provided financial support for AMB. The US Forest Service Starkey Experimental Forest and Range allowed access to their property. The Pacific Northwest Research Station (USDA Forest Service) provided financial and logistical support for BAE. The Eastern Oregon Agricultural Research Center—Union provided logistical support for AMB. Oregon State University at Eastern Oregon University allowed us to use their greenhouse facilities. This research was funded by a grant from the Center for Invasive Plant Management to BAE. This manuscript was improved by comments from David Eldridge, Pat Kennedy and two anonymous reviewers.

Appendix. Complete list of species and the number of seeds identified in cattle, elk, and deer feces from two study areas in northeastern Oregon during 2005

	Cattle ($N = 20$)	Elk ($N = 20$)	Deer ($N = 10$)
Exotic forb species			
Alyssum alyssoides	2	–	–
Cerastium glomeratum	13	6	2
Medicago lupulina	3	–	–
Potentilla recta	–	–	1
Rumex acetosella	19	12	–
Stellaria media	1	27	–
Taraxacum officinale	–	–	1
Thlaspi arvense	–	2	1
Trifolium hybridum	1	3	–
Trifolium repens	3	6	–
Trifolium sp.	1	–	–
Veronica arvensis	15	2	–
Veronica chamaedrys	2	–	–

Native forb species			
Cerastium arvense	20	67	–
Chenopodium leptophyllum	3	–	–
Colomia linearis	1	1	–
Epilobium watsonii var. *occidentalis*	3	1	–
Erigeron corymbosus	3	–	–
Erigeron peregrinus	8	–	–
Frageria vesca	–	1	–
Grindelia nana	2	–	1
Mitella stauropetala	–	1	–
Oxalis corniculata	1	–	–
Oxalis stricta	5	–	–
Plantago major	1	–	–
Potentilla glandulosa	–	5	1
Prunella vulgaris	2	3	–
Ranunculus uncinatus	4	1	–
Sanguisorba annua	1	–	2
Stellaria longipes	1	–	–
Urtica dioeca	2	–	–
Achillea millefolium	5	1	–
Oxalis spp.	1	–	–
Agastache urticifolia	7		–
Exotic graminoid species			
Agrostis gigantea	4	–	–
Apera interrupta	2	4	–
Bromus inermus	6	1	–
Dactylus glomerata	1	–	–
Festuca ovina	2	1	–
Myosotis stricta	2	–	–
Poa compressa	18	5	–
Poa pratensis	310	72	5
Native graminoid species			
Bromus carinatus	16	2	2
Carex spp.	4	4	–
Danthonia intermedia	1	–	–
Deschampsia caespitosa	1	–	–
Festuca idahoensis	–	2	–
Festuca occidentlis	2	2	4
Koelaria cristata	7	6	–
Myosotis stricta	–	–	1
Native shrub and vine species			
Physocarpus malvaceus	–	1	–
Lonicera involucrata	–	1	–

References

Barnes, T.G., Varner, L.W., Blakenship, L.H., Gallagher, J.F., 1992. Indigestible particulate passage in white-tailed deer. In: Brown, R.D. (Ed.), The Biology of Deer. Springer, New York, pp. 436–442.

Brooks, M.L., Matchett, J.R., Berry, K.H., 2006. Effects of livestock watering sites on alien and native plants in the Mojave Desert, USA. Journal of Arid Environments 67, 125–147.

Carpinelli, M.F., Schauer, C.S., Bohnert, D.W., Hardegree, S.P., Falck, S.J., Svejcar, T.J., 2005. Effect of ruminal incubation on perennial pepperweed germination. Rangeland Ecology Management 58, 632–636.
Cosyns, E., DelPorte, A., Lens, L., Hoffmann, M., 2005a. Germination success of temperate grassland species after passage through ungulate and rabbit guts. Journal of Ecology 93, 353–361.
Cosyns, E., Claerbout, S., Lamoot, I., Hoffmann, M., 2005b. Endozoochorous seed dispersal by cattle and horse in a spatially heterogeneous landscape. Plant Ecology 178, 149–162.
Couvreur, M., Christiaen, B., Verheyen, K., Hermy, M., 2004. Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. Applied Vegetation Science 7, 229–236.
Couvreur, M., Cosyns, E., Hermy, M., Hoffmann, M., 2005. Complimentarity of epi- and endozoochory of plant seeds by free-ranging donkeys. Ecography 28, 37–48.
DelCurto, T., Porath, M., Parsons, C.T., Morrison, J.A., 2005. Management strategies for sustainable beef cattle grazing on forested rangelands in the Pacific Northwest. Rangeland Ecology Management 58, 119–127.
Doucette, K.M., Wittenberg, K.M., McCaughey, W.P., 2001. Seed recovery and germination of reseeded species fed to cattle. Journal of Range Management 54, 575–581.
Dwyer, D.D., 1961. Activities and grazing preferences of cows with calves in northern Osage County Oklahoma. Oklahoma Agricultural Experiment Station Bulletin B-588, 61pp.
Ford, W.M., Madarish, D., Schuler, T.M., Castleberry, S.B., 2003. Influence of white-tailed deer digestion on running buffalo clover (*Trifolium stoloniferum*: Fabaceae Muhl. Ex A. Eaton) germination. American Midland Naturalist 149, 425–428.
Fredrickson, E.L., Estell, R.E., Havstad, K.M., Ksiksi, T., Van Tol, J., Remmenga, M.D., 1997. Effects of ruminant digestion on germination of Lehmann love-grass seed. Journal of Range Management 50, 20–26.
Gardener, C.J., McIvor, J.G., Jansen, A., 1993. Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. Journal of Applied Ecology 30, 63–74.
Gill, R.M.A., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74, 210–218.
Hitchcock, C.L., Cronquist, A., 1973. Flora of the Pacific Northwest: An Illustrated Manual. University of Washington Press, Seattle, WA, USA.
Janzen, D.H., 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. American Naturalist 123, 338–353.
Johnson, B.K., Kern, J.W., Wisdom, M.J., Findholt, S.L., Kie, J.G., 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64, 685–697.
Malo, J.E., Suárez, F., 1998. The dispersal of a dry-fruited shrub by red deer in a Mediterranean ecosystem. Ecography 21, 204–211.
Malo, J.E., Jiménez, B., Suárez, F., 2000. Herbivore dunging and endozoochorous seed deposition in a Mediterranean *dehesa*. Journal of Range Management 53, 322–328.
Milne, J.A., MacRae, J.C., Spence, A.M., Wilson, S., 1978. A comparison to the voluntary intake and digestion of a range of forages at different times of the year by sheep and red deer. British Journal of Nutrition 40, 347–357.
Milton, S.J., Dean, W.R.J., 2001. Seeds dispersed in dung of insectivores and herbivores in semi-arid southern Africa. Journal of Arid Environments 47, 465–483.
Myers, J.A., Vellend, M., Gardescu, S., Marks, P.L., 2004. Seed dispersal by white-tailed deer: implications for long distance dispersal, invasion, and migration of plants in eastern North America. Oecologia 139, 35–44.
Ocumpaugh, W.R., Archer, S., Stuth, J.W., 1996. Switchgrass recruitment from broadcast seed vs. seed fed to cattle. Journal of Range Management 49, 368–371.
Olson, B.E., Wallander, R.T., Kott, R.W., 1997. Recovery of leafy spurge seed from sheep. Journal of Range Management 50, 10–15.
Pakeman, R.J., 2001. Plant migration rates and seed dispersal mechanisms. Journal of Biogeography 28, 795–800.
Parsons, C.T., Momont, P.A., DelCurto, T., McInnis, M., Porath, M.L., 2003. Cattle distribution patterns and vegetation use in mountain riparian areas. Journal of Range Management 56, 334–341.
Radford, I.J., Nicholas, D.M., Brown, J.R., Kriticos, D.J., 2001. Paddock-scale patterns of seed production and dispersal in the invasive shrub *Acacia nilotica* (Mimosaceae) in northern Australian rangelands. Austral Ecology 26, 338–348.
Ramos, M.E., Robles, A.B., Castro, J., 2006. Efficiency of endozoochorous seed dispersal in six dry-fruited species (Cistaceae): from seed ingestion to early seed establishment. Plant Ecology 185, 97–106.
Roath, L.R., Krueger, W.C., 1982. Cattle grazing and behavior on a forested range. Journal of Range Management 35, 332–338.
Rogers, L.L., 1987. Seasonal changes in defecation rates of free-ranging white-tailed deer. Journal of Wildlife Management 51, 330–333.
Rowland, M.M., Bryant, L.D., Johnson, B.K., Noyes, J.H., Wisdom, M.J., Thomas, J.W., 1997. The Starkey Project: history, facilities, and data collection methods for ungulate research. USDA Forest Service General Technical Report PNW-GTR-396.
Rowland, M.M., Coe, P.K., Stussy, R.J., Ager, A.A., Cimon, N.J., Johnson, B.K., Wisdom, M.J., 1998. The Starkey habitat data base for ungulate research: construction, documentation, and use. USDA Forest Service General Technical Report PNW-GTR-430.
Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64, 672–684.
SAS Inc., 2002. SAS Institute, Cary, NC, USA.
Schommer, T., Johnson, B., 2003. Analysis of Elk Statistics 1965–2001 Wallowa, Wenaha-Snake and Umatilla-Whitman Provinces. USDA Wallowa-Whitman National Forest, Baker City, OR.
Skovlin, J.M., 1991. Fifty years of research progress: a historical document on the Starkey Experimental Forest and Range. USDA Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-266, Portland, OR.

Szmenthy, L., Ritter, D., Heltai, M., 1994. Preliminary results of radio-tracking of red deer (*Cervus elaphus*) in Hungary. In: Milne, J.A. (Ed.), Recent Developments in Deer Biology. Macaulay Land Research Institute, Aberdeen, UK, p. 281.

Tate, K.W., Atwill, E.R., McDougald, N.K., George, M.R., 2003. Spatial and temporal patterns of cattle feces deposition on rangeland. Journal of Range Management 56, 432–438.

Traba, J., Levassor, C., Peco, B., 2003. Restoration of species richness in abandoned Mediterranean grasslands: seeds in cattle dung. Restoration Ecology 11, 378–384.

Vellend, M., 2002. A pest and an invader: white-tailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). Natural Areas Journal 22, 230–234.

Vellend, M., Myers, J.A., Gardescu, S., Marks, P.L., 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. Ecology 84, 1067–1072.

Vilà, M., D'Antonio, C.M., 1998. Fruit choice and seed dispersal of invasive vs. noninvasive *Carpobrotus* (Aizoaceae) in coastal California. Ecology 79, 1053–1060.

Wagnon, K.A., 1963. Behavior of beef cows on a California range. California Agricultural Experiment Station Bulletin 799, 59pp.

Wald, E.J., Kronberg, S.L., Larson, G.E., Johnson, W.C., 2005. Dispersal of leafy spurge (*Euphorbia esula* L.) seeds in the feces of wildlife. American Midland Naturalist 154, 342–357.

Wallander, R.T., Olson, B.E., Lacey, J.R., 1995. Spotted knapweed seed viability after passing through sheep and mule deer. Journal of Range Management 48, 145–149.

Wallowa Whitman National Forest, 2001. Grazing statistics. Unpublished Report. On file at the Wallowa-Whitman National Forest Headquarters, Baker City, OR.

Wisdom, M.J. (Technical editor), 2005. The Starkey project: a synthesis of long-term studies of elk and mule deer. Alliance Communications Group, Lawrence, KS.