

## Seed dispersal by *Bison bison* in a tallgrass prairie

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### Abstract.

**Question:** To what extent do bison serve as seed dispersers via epizoochory and endozoochory in tallgrass prairie, and does this differ by age-sex class of bison and by month?

**Location:** Tallgrass Prairie Preserve, Osage County, Oklahoma, USA.

**Methods:** We collected bison hair from 19 bulls, 45 cows, and 47 juveniles in fall and we collected bison dung monthly for a year. We recovered and identified seeds from hair and dung samples, and classified seeds by size and diaspore characteristics.

**Results:** Bison hair samples contained 2768 seeds from at least 76 plant species. Several species found in hair did not feature specialized appendages for adhesive dispersal. Seed species composition differed in hair collected from bulls, cows and juveniles, possibly due to differential habitat use. Dung samples contained 7418 seeds from at least 70 species, from which graminoids accounted for 3936 seeds from 27 species. Species composition of seeds contained in dung samples differed among months, corresponding to availability. Grasses constituted about half the seeds in both dung and hair samples, but *Asteraceae* were more strongly represented in hair, while *Scrophulariaceae* and *Solanaceae* were more strongly represented in dung.

**Conclusions:** We conclude that bison are potentially important dispersers of forbs as well as graminoids. A high abundance and wide diversity of seeds were found in both bison hair and dung. The great majority of seeds found undamaged in bison dung were small seeds, which agrees with the 'foliage is the fruit' hypothesis. Dispersal by both epizoochory and endozoochory may play an important role in life history of many species in tallgrass prairie landscapes.

**Keywords:** Dung sample; Endozoochory, Epizoochory; Hair sample; Herbivore; Ungulate.

**Nomenclature:** Kartesz & Kartesz (1980).

### Introduction

Zoochory, dispersal by animals, is potentially directed dispersal because animals are habitat-selective, thereby increasing the probability that seeds are placed in a habitat similar to that of the parents (Kiviniemi & Eriksson 1999). Epizoochory is dispersal by adhesion to fur, feathers, or feet of animals. Although it has been widely assumed that plants adapted to epizoochory usually have seeds with adhesive mechanisms (spines, hooks or viscid exudates) that facilitate attachment to fur or feathers (van der Pijl 1982), effective epizoochory does not require such mechanisms (Fischer et al. 1996).

Endozoochory is the dispersal of fruits or seeds that pass unharmed through digestive tracts of animals. Van der Pijl (1982) considered it adaptive when seeds are adapted to fruit-eating animals, but accidental when seeds are indiscriminately ingested with foliage. Accordingly, most endozoochory studies have focused on animals consuming fleshy fruits. However, Janzen (1984) proposed the 'foliage is the fruit' hypothesis, suggesting foliage may attract dispersal agents in small-fruited herbaceous plants, such as grasses. This hypothesis has been supported by studies in Europe and North America (Malo & Suárez 1995a; Quinn et al. 1994; Ortmann et al. 1998).

Tallgrass prairie, one of the most fragmented biomes of North America; has been reduced to < 5% of that of pre-European settlement (Samson & Knopf 1994). Fire, drought, and bison (*Bison bison*) grazing were major forces shaping tallgrass prairie (Knapp et al. 1999). It is reasonable to suspect that bison could serve as seed dispersers, both by external and internal means, of plant species in tallgrass prairie. Obtaining information about seed dispersal by bison will increase our understanding of ecological processes occurring in the tallgrass prairie, and can therefore improve conservation and restoration of remaining tracts of this ecosystem.

The purpose of this study was to determine the extent to which bison act as agents of plant dispersal via epizoochory and endozoochory in a tallgrass prairie. We examined hair of free-ranging bison for the presence and abundance of seeds. Seed composition in bison hair may be influenced by sex because male and female bison segregate in different groups most of the year and show different grazing patterns (Coppedge & Shaw 1998a). We evaluated whether composition of seeds recovered from bison hair samples differs among age-sex groups (bulls, cows, juveniles). We also recovered seeds from dung pats of mixed age-sex groups of bison collected monthly, and tested whether the number and composition of seed species in bison dung differs among months.

## Methods

### Study area

The Tallgrass Prairie Preserve, owned by The Nature Conservancy, is located in Osage County, Oklahoma (36°50' N, 96°25' W). More than 750 vascular plant species have been documented from this 15 410-ha preserve (Palmer 2007). Warm-season grasses, *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, *Schizachyrium scoparium* and *Sporobolus compositus* dominate the vegetation (Hamilton 1996; Palmer et al. 2000). *Carex* spp. are subdominant graminoids, and *Ambrosia psilostachya* and *Amphiachyris dracunculoides* are common forbs (Coppedge 1996). A 2250-ha bison enclosure is burned in patches, ca. 30% burned annually, which, in combination with unrestricted selection by bison, creates a shifting mosaic of vegetation structure and composition (Hamilton 1996; Fuhlendorf & Engle 2001, 2004).

### Epizoochory study

The epizoochory samples were obtained in the fall of 2000 and 2001 during the annual bison roundup, which is conducted to census and vaccinate bison against brucellosis. Since bison are wild and unpredictable, sampling their hair is only feasible when they are physically restrained. Thus, sampling for epizoochory is restricted to the fall. While in a squeeze chute (necessary for restraint), hair samples were clipped from a small portion of the forehead of each bison ( $n = 45$  cows, 19 bulls, and 47 juveniles) as close to the skin as possible. We searched hair samples for seeds under magnification, and saved the seeds for subsequent counting and identification. We

examined seeds under a stereomicroscope for identification based on manuals (Davis 1993; Delorit 1970; Martin & Barkley 1961; Montgomery 1977) and the seed collection of the Oklahoma State University herbarium. Damaged seeds were discarded. We classified diaspores (seeds plus the pericarp, glumes, bracts or other structures typically attached while being dispersed) according to size ( $< 2$  mm, 2-4 mm,  $> 4$  mm) and morphology (with clear attachment mechanism such as hooks, with projections not clearly related to attachment such as unhooked awns, smooth, or with fleshy fruits). Seeds were identified to genus or species level and seed abundance was expressed on a per gram of hair basis.

We subjected the data to redundancy analysis (RDA), a type of multivariate regression suitable for species composition (ter Braak & Prentice 1988). We used CANOCO 4 (ter Braak & Šmilauer 1998) to perform RDA on the relative abundance of seeds using bulls, cows, and juveniles as nominal explanatory variables and year as a covariate (equivalent to a factor with two levels). We used the default options of CANOCO 4, except that we square-root transformed species data. We performed permutation tests (999 permutations) to assess significance. Seeds that we could not identify to species were included in the analysis as a member of one of three groups: grass seeds, seeds from family *Asteraceae*, and seeds from an unknown family.

### Endozoochory study

We collected dung from bison ( $n=12$ ) monthly from January through December 2001 (total of 144 samples). During each collection date we followed the first cow or cow-juvenile group we met ( $\geq 10$  bison) on foot from the main roads inside the Tallgrass Prairie Preserve, and we collected fresh dung from a group immediately after the group departed an area. We did not collect dung from bulls, which represented a small proportion of the herd. Since we were able to ascertain the freshness of the dung as well as the composition of the bison groups, we are confident that there are no dung samples from bulls. To avoid collecting seeds from the soil bank, we excluded dung in direct soil contact. Dung samples were brought to the laboratory in marked plastic bags. We washed 50g of each sample under tap water in a set of sieves (1.8 mm, 1.0 mm, and 500  $\mu$ m screen sizes) to recover seeds, which were dried at ca. 35 °C for 12 to 24 h. Seeds were sorted by species under magnification, and damaged seeds were discarded. We classified seeds to size and morphology as described in the previous section. We used an additional set of

dung samples to grow plants from seeds to assist in identification.

We used both univariate and multivariate methods to analyze data after first testing for homogeneity of variance (Levene's test). We used analysis of variance (proc GLM of SAS) to test for differences in number of species and seed abundance (number of seeds per gram of dung dry matter) in samples across months. When I tests were significant ( $\alpha = 0.05$ ) we performed multiple mean comparisons tests using the Bonferroni method. We log-transformed abundance because heterogeneity of variance was detected in seed abundance.

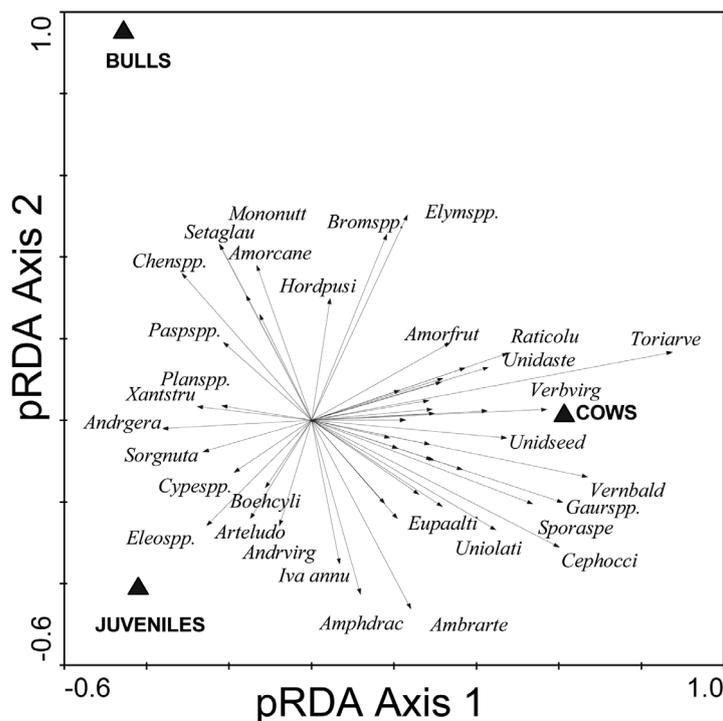
We used RDA to analyse relative abundance of seeds in CANOCO 4 (ter Braak & Šmilauer 1998) with months as nominal explanatory variables as described for the epizoochory study. The default options were followed, except that species data were square-root transformed. Seeds not identified were included in the analysis in three groups as described for the epizoochory study.

## Results

### Epizoochory

We found 2768 seeds from at least 76 plant species (4% could not be identified) in 111 hair samples from bison in both 2000 and 2001 (Table 1). Only 2 of 111 hair samples contained no seeds. 46.1% of diaspores were graminoids, of which the majority belonged to the *Poaceae* (Table 2). *Asteraceae*, *Fabaceae* and *Apiaceae* (largely *Torilis arvensis*) were also well represented. Several species not native to the US, in particular *Bromus* spp. and *Torilis arvensis*, were found in bison hair. Only 17.5% of the diaspores had obvious attachment mechanisms (hooked hairs or barbs). The majority (70.9%) had projections that were not stereotypical for animal dispersal. Smooth seeds and fleshy fruits were infrequent, and most were larger than 4mm.

As would be expected, some species with adhesive appendages, such as *Xanthium strumarium*, *Torilis arvensis*, and *Desmodium sessilifolium*, were abundant in bison hair samples. However, many abundant species in bison hair (e.g. *Andropogon gerardii*, *Sorghastrum nutans*, *Vernonia baldwinii*, *Solidago* spp., *Aster* spp.)



**Fig. 1.** Bi-plot showing the first two axes of a partial RDA of seed species found in bison hair. Centroids of nominal explanatory variables (bulls, cows, and juveniles, represented by triangles) are plotted with species (represented by arrows) of seeds present in bison hair. Monte Carlo permutation tests were significant for the first (eigenvalue = 0.032,  $p = 0.001$ ) and all canonical axes (eigenvalue = 0.047,  $p = 0.001$ ). Codes represent the first four letters of genera and species (Table 1).

**Table 1.** Species of seeds most commonly found in bison hair samples ( $N = 111$ ) and bison dung pats ( $N = 144$ ) at the Tallgrass Prairie Preserve, Oklahoma. Diaspore length represents the estimated median length of the dispersed unit (e.g. seed, seed plus pericarp; seed plus glumes, etc.): S: small or less than 2 mm; M: medium or between 2 and 4 mm; L: Large, or greater than 4mm. Diaspore types: A = with obvious structures for attachment such as hooked hairs or adhesive pads, P = with awns, glumes, hairs, or pappus that could potentially (but do not obviously) serve a function in attachment, F = with a fleshy fruit, and S = without hairs, projections, or fleshy fruits.

Species	Family	Diaspore length	Diaspore type	Total nr. of seeds in hair samples	Nr. of hair samples with species	Total nr. of seeds in dung samples	Nr. of dung samples with species
<i>Ambrosia artemisiifolia</i>	Asteraceae	M	P	78	23	0	0
<i>Ambrosia</i> spp.	Asteraceae	M	P	1	1	32	13
<i>Amorpha fruticosa</i>	Fabaceae	L	P	45	17	0	0
<i>Amphiachyris dracunculoides</i>	Asteraceae	S	P	93	29	0	0
<i>Andropogon gerardii</i>	Poaceae	L	P	622	67	12	1
<i>Artemisia ludoviciana</i>	Asteraceae	S	P	2	1	335	21
<i>Aster</i> spp.	Asteraceae	M	P	63	28	0	0
<i>Boehmeria cylindrica</i>	Urticaceae	S	P	94	14	0	0
<i>Bromus</i> spp. <sup>b</sup>	Poaceae	L	P	331	65	394	94
<i>Capsella bursa-pastoris</i> <sup>a</sup>	Brassicaceae	L	S	0	0	112	12
<i>Carex</i> spp.	Cyperaceae	M	P	5	5	166	75
<i>Cephalanthus occidentalis</i>	Rubiaceae	L	S	71	19	0	0
<i>Chaerophyllum tainturieri</i>	Apiaceae	L	P	2	2	69	19
<i>Chamaesyce maculata</i>	Euphorbiaceae	S	S	0	0	37	9
<i>Cynodon dactylon</i> <sup>a</sup>	Poaceae	M	P	10	6	1190	87
<i>Cyperus</i> spp.	Cyperaceae	M	P	2	2	52	29
<i>Desmodium sessilifolium</i>	Fabaceae	L	A	65	26	0	0
<i>Digitaria</i> spp.	Poaceae	M	P	5	5	60	24
<i>Eleocharis</i> spp.	Cyperaceae	S	S	4	3	139	27
<i>Elymus</i> spp.	Poaceae	L	P	47	30	7	7
<i>Eragrostis</i> spp.	Poaceae	M	S	0	0	80	24
<i>Eupatorium altissimum</i>	Asteraceae	M	P	16	6	0	0
<i>Gaura</i> spp.	Onagraceae	M	P	15	8	1	1
<i>Hedyotis nigricans</i>	Rubiaceae	S	P	0	0	134	35
<i>Helenium autumnale</i>	Asteraceae	M	P	38	22	0	0
<i>Hordeum pusillum</i>	Poaceae	L	A	17	11	10	10
<i>Iva annua</i>	Asteraceae	M	S	65	20	3	2
<i>Krigia cespitosa</i>	Asteraceae	S	P	0	0	67	11
<i>Lepidium densiflorum</i>	Brassicaceae	M	S	1	1	60	32
<i>Medicago lupulina</i> <sup>a</sup>	Fabaceae	M	P	0	0	156	42
<i>Melilotus officinalis</i> <sup>a</sup>	Fabaceae	M	P	16	9	13	9
<i>Monolepis nutallii</i>	Chenopodiaceae	S	S	5	2	0	0
<i>Oxalis stricta</i>	Oxalidaceae	S	S	1	1	32	26
<i>Panicum capillare</i>	Poaceae	S	S	0	0	36	21
<i>Panicum obtusum</i>	Poaceae	M	S	0	0	21	18
<i>Panicum</i> spp.	Poaceae	M	P	24	16	65	26
<i>Plantago</i> spp.	Plantaginaceae	S	S	2	2	162	47
<i>Schizachyrium scoparium</i>	Poaceae	L	P	23	15	0	0
<i>Silene antirrhina</i>	Caryophyllaceae	L	A	0	0	38	15
<i>Solanum carolinense</i>	Solanaceae	L	F	0	0	827	39
<i>Solidago</i> ssp.	Asteraceae	M	P	102	32	0	0
<i>Sorghastrum nutans</i>	Poaceae	L	P	53	29	1	1
<i>Sphenopholis obtusata</i>	Poaceae	M	P	0	0	79	11
<i>Sporobolus compositus</i>	Poaceae	S	S	11	9	1395	61
<i>Symphoricarpos orbiculatus</i>	Caprifoliaceae	L	F	0	0	46	10
<i>Torilis arvensis</i> <sup>a</sup>	Apiaceae	L	H	163	36	11	9
<i>Tridens flavus</i>	Poaceae	S	P	61	22	0	0
<i>Verbesina virginica</i>	Asteraceae	L	P	28	14	0	0
<i>Vernonia baldwinii</i>	Asteraceae	M	P	114	31	0	0
<i>Veronica peregrina</i>	Scrophulariaceae	M	S	0	0	806	32
<i>Viola</i> spp.	Violaceae	S	S	0	0	40	11
<i>Vulpia octoflora</i>	Poaceae	L	P	6	6	135	47
<i>Xanthium strumarium</i>	Asteraceae	L	A	207	50	0	0

<sup>a</sup>Introduced species (not native to the USA)

<sup>b</sup>Genus with some native and some introduced species, but introduced species are more common in these data

are suspected to be largely wind-dispersed, and other frequent species to not have clear attachment mechanisms (Tables 1, 2).

Species composition of seeds in bison hair differed significantly among age-sex classes of bison (Fig. 1). Plants typically occurring in areas with much bare soil (such as *Chenopodium* spp. and *Monolepis nutallii*) are associated with bulls. Low-fruited wetland plants (*Boehmeria cylindrica*, *Eleocharis* spp. and *Cyperus* spp.) were found on juveniles, while wetland shrubs (*Amorpha fruticosa* and *Cephalanthus occidentalis*) were found on cows. *Torilis arvensis*, with small hooks, was found predominantly on cows while *Xanthium strumarium*, with large hooks, was rarely found on cows. We could not interpret other patterns of association between seeds and bison age-sex classes.

### Endozoochory

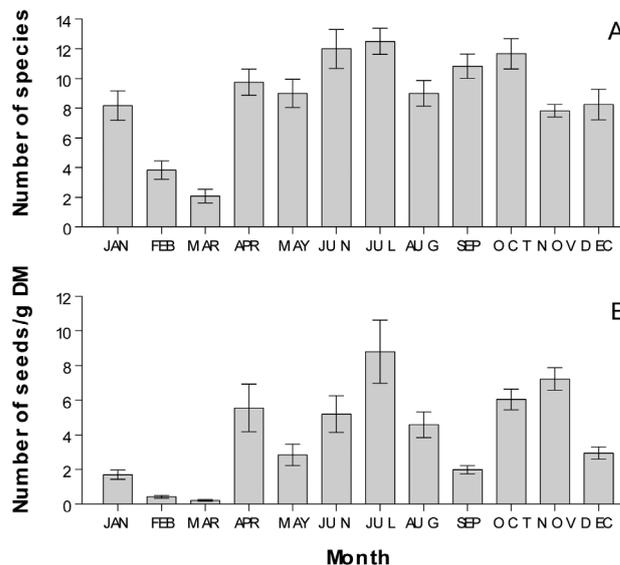
Of 7418 seeds we found in bison dung samples, we identified 94% to at least genus level (70 species from 23 families, Table 1). Graminoids were represented by 27 species (39% of the total species) with a total of 3936 seeds (53% of the total number of seeds).

The dominant families were the *Poaceae*, *Solanaceae*, and *Scrophulariaceae* (Table 2). Most diaspores had some sort of projection, but few possessed traits stereotypically related to epizoochory. Only 4% of the diaspores were associated with fleshy fruits. More than a third of the diaspores were smooth, and most were less than 4mm in size. Only 2 dung samples, collected in March, contained no seeds. Also, number of species, which ranged from an average of about 2 to 12 per dung pat, differed by month ( $F = 12.52$ ,  $df = 11$ ,  $p < 0.0001$ ). Dung from February and March contained similarly low numbers of species ( $p = 0.1659$ ), and the fewest number of seed species of any of the months (Fig. 2A). Richness was greatest in June and July (Fig. 2A). Abundance (number of seeds /g of dung dry matter), which also varied monthly ( $F = 28.11$ ,  $df = 11$ ,  $p < 0.0001$ ), was lowest in February and March and greatest in July (Fig. 2B).

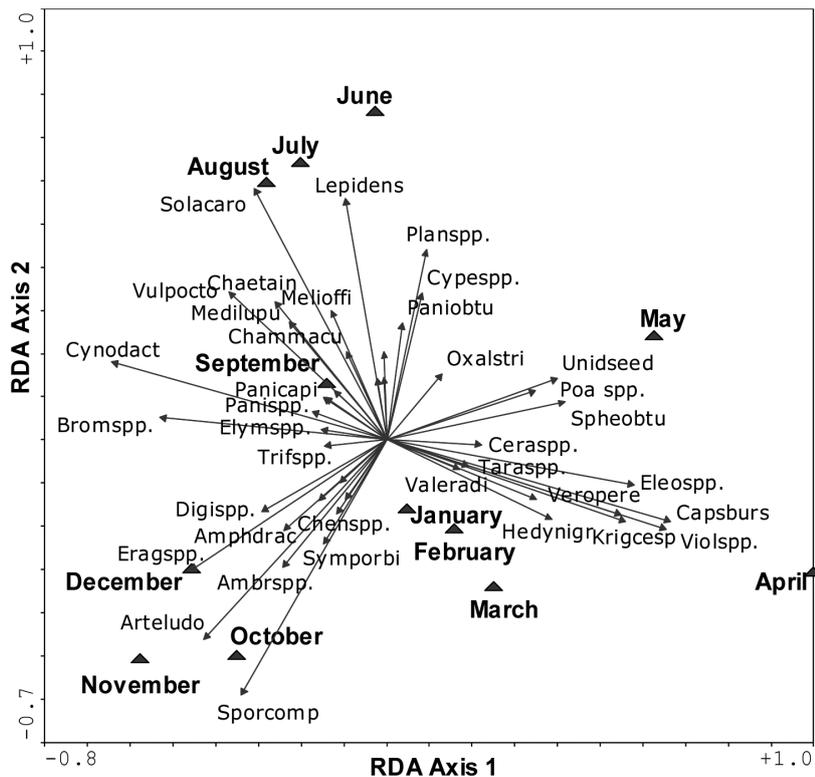
Species composition of seeds from dung differed among months, tracing a counterclockwise path through ordination space (Fig. 3). Not surprisingly, this related to fruiting time. Spring-fruited species such as *Capsella bursa-pastoris*, *Carex* spp., *Viola* spp., *Eleocharis* spp., *Krigia cespitosa*, *Hedyotis nigricans*, and *Veronica peregrina*, were found in April. Samples from May had late spring-fruited *Poa* spp. and *Sphenopholis obtusata*. June, July, and August samples had summer-fruited *Solanum carolinense*

**Table 2.** Diaspore families, characteristics, and size, expressed as a percentage of total seeds encountered in the two studies. Characteristics and size are considered median or ‘typical’ for the species: for example, a grass seed may sometimes be encountered unadorned but be more commonly dispersed as part of a spikelet with a long glume. Similarly, seeds in the *Asteraceae* may or may not have a pappus attached. ‘Unknown’ means the dominant form cannot be easily assessed. Proportions differ in all cases (Plant family:  $\chi^2 = 1911$ ,  $p < 0.0001$ , Diaspore characteristics:  $\chi^2 = 761$ ,  $p < 0.0001$ , Diaspore size:  $\chi^2 = 1606$ ,  $p < 0.0001$ )

	Hair	Dung
<b>Plant family</b>		
<i>Asteraceae</i>	32.2%	6.6%
<i>Solanaceae</i>	0.0%	11.3%
<i>Poaceae</i>	45.6%	48.5%
<i>Scrophulariaceae</i>	0.0%	11.0%
<i>Fabaceae</i>	5.1%	2.7%
<i>Apiaceae</i>	6.3%	1.1%
Other	10.8%	18.8%
<b>Diaspore characteristics</b>		
Attachment mechanisms obvious	17.5%	3.5%
Projections not clearly related to attachment	70.9%	48.2%
Smooth	6.8%	35.7%
Fleshy	0.1%	4.0%
Unknown	4.6%	8.6%
<b>Diaspore size</b>		
Large (> 4 mm long)	63.7%	23.2%
Medium (2-4 mm long)	21.4%	38.9%
Small (< 2 mm long)	10.4%	35.4%
Unclear	4.6%	2.6%



**Fig. 2. a.** Mean number of species of seed found in pats ( $n = 12$ ) of bison dung collected monthly during 2001. Vertical bars are one standard error of the mean. **b.** Mean abundance (number of seeds/g of dung dry matter) of seeds found in bison dung ( $n = 12$ ) collected monthly during 2001.



**Fig. 3.** Bi-plot showing the first two axes of an RDA of seed species found in bison dung across months. Monte Carlo permutation tests were significant for the first (eigenvalue = 0.116,  $F = 17.126$ ,  $p = 0.001$ ) and all canonical axes (eigenvalue = 0.372,  $F = 6.999$ ,  $p = 0.001$ ). Centroids (represented by triangles) of nominal explanatory variables (months) are plotted with species of seeds (represented by arrows). Species codes are the first four letters of the genus and species names (Table 1).

and *Lepidium densiflorum*. Species composition of September dung samples was intermediate between summer and late fall samples. *Bromus* spp. and *Cynodon dactylon* were most closely associated with September samples. Dung samples from October through December were similar, and contained fall-fruited *Eragrostis* spp., *Artemisia ludoviciana*, and *Sporobolus compositus*. In contrast, January, February and March were similar to each other, but were associated less positively with any particular plant species than other months, possibly reflecting the few seeds recovered in dung pats collected early in the year.

#### *Epizoochory vs. endozoochory*

Differences in methodology and season of sampling preclude a rigorous test of differences between epizoochory and endozoochory. However, strong differences appear between the hair and dung samples (Tables 1, 2). Some species with hooked hairs (e.g. *Xanthium strumarium*, *Desmodium sessilifolium*) are found exclusively in hair. Two of the dominant prairie grasses (*Andropogon gerardii*,

*Sorghastrum nutans*) and abundant fall-blooming forbs (*Solidago* spp, *Vernonia baldwinii*, *Ambrosia artemisiifolia*, *Aster* spp.) also predominate in hair samples. Their sheer abundance in the fall, plus their tall stature, may explain their abundance in bison hair samples more than physical characteristics of the diaspores. The distinction between dung and hair is not merely seasonal, because fall-sampled dung is compositionally distinct from hair (RDA biplot not shown).

The dominant category of seeds for both dung and hair is those with projections not clearly related to attachment (Table 2). Seeds from hair are more likely to have obvious attachment mechanisms, and less likely to have smooth seeds, than those from dung. Seeds from dung are typically smaller than those from hair. This pattern is unlikely to result from a sampling bias, because small seeds are much harder to find in dung than in hair.

## Discussion

Our findings of high abundance and diversity of seeds in bison hair support observations by Berthoud (1892) who also found seeds from many species on bison hair. Other investigators have found similar numbers of plant species carried in fur or hair of mammals. Seeds of 85 vascular plant species were found in fleece of sheep in calcareous grasslands of Germany (Fischer et al. 1996). Milton et al. (1990) found seeds of at least 54 plant species in fleece of sheep in Karoo rangelands of South Africa.

Sampling in this study was limited to hair from the head where presumably most seeds were attached while animals were grazing, wallowing or lying. However, seeds from *Andropogon*, *Sorghastrum*, and *Vernonia* may be presented at heights greater than 1m, and therefore might have been acquired while walking. Seed composition might differ in hair from other body parts and seasons. Fischer et al. (1996) found most seeds attached to the breast and neck of sheep. This pattern might also occur in bison, but sampling these body areas is infeasible with bison for safety reasons. Nevertheless, our study provides a good evidence of the diversity of species likely to attach to bison hair and to be dispersed by this mechanism in the tallgrass prairie.

Our finding of high abundance of species without clear attachment mechanisms is a result consistent with other studies (e.g. Fischer et al. 1996; Kiviniemi & Eriksson 1999; Couvreur et al. 2004, 2005b; Moussie et al. 2005).

How seed dispersal by bison influences distribution and abundance of these introduced species in tallgrass prairie is unknown. Constible et al. (2005) studied the dispersal of seeds by introduced bison on Santa Catalina Island, California, and found that non-native forbs predominated in bison hair (possibly because non-native forbs dominate the vegetation). Because of that and the fact that bison were also introduced to the island, the authors discussed the negative impact bison could have on the ongoing efforts to restore the native island flora. Also, the fact that cattle are considered major dispersers of some noxious introduced plants (Clerck-Floate 1997; Tews et al. 2004) may indicate that more attention should be given to this subject.

Difference among sex and age groups in seed composition are difficult to explain, but there are some interpretable patterns. For example, bison bulls wallow more than females and juveniles (McMillan et al. 2000), potentially explaining why plant species occurring in bare soil are associated with bulls. The association between some wetland plants and juveniles and cows implies a possible habitat segregation that is worth examining further. The relative stature of juveniles and cows might explain why

wetland herbs are associated with juveniles while wetland shrubs are associated with cows. The positive association of cows with the small-hooked *Torilis arvensis* and the negative association of the large-hooked *Xanthium strumarium* are consistent with the higher density of fine hairs on cows (Peters & Slen 1964).

Bison typically exhibit sexual segregation in foraging habits, and the selection is expressed at the diet and landscape levels (Coppedge & Shaw 1998a; Post et al. 2001). Bison prefer graminoids (Coppedge et al. 1998b), but mature males select diets with higher proportions of C4 grasses than do other bison (Post et al. 2001). Interestingly, in our study bison bulls had relatively few C4 grass seeds in their hair (15% as opposed to 24% for cows and 49% for juveniles). Groups of mature males spatially segregate from groups of mature cows and juveniles, by their preference/avoidance of burned patches within and between seasons (Coppedge and Shaw 1998a). Females search for highly preferred and limited cool-season graminoids (Coppedge and Shaw 1998b) that are more available in recently disturbed patches during the winter months. These documented behavioral differences are not clearly reflected in the compositional patterns of Fig. 1.

Ours is not the only study that has shown sexual differences in epizoochory. Female hares (*Lepus capensis*) in Africa carried three times more seeds on their fur than males, probably due to different grooming behavior between sexes (Agnew & Flux 1970).

Even though forbs contribute more than grasses to plant species richness in tallgrass prairie vegetation, grass biomass is greater than forb biomass (Collins & Glenn 1991). We were thus surprised by the variety and number of forb seeds in bison dung, especially given the results of microhistological fecal analysis (Coppedge & Shaw 1998b) implying forbs never represent more than 1% of bison diet in tallgrass prairie. One explanation could be that the microhistological analyses could misrepresent forbs if they have higher digestibility than grasses and sedges. It is also possible that even if forb foliage represents a small portion of the diet, fruiting structures of forbs may be preferentially consumed.

The number of non-graminoid seeds occurring in dung (Fig. 3, Tables 1, 2) is interesting because bison are thought to be pure grass specialists (Coppedge et al. 1998b). It is likely that some small-seeded and small-statured plant species are incidentally consumed while bison are foraging on grasses. However, seeds from *Solanum carolinense*, which has large fruits, are not likely to be explained by incidental consumption. The notion that bison are partially frugivorous warrants further investigation.

Bison are similar to other herbivores in having many

species in dung. In a Mediterranean grassland, Malo & Suárez (1995a) found between 52 and 78 plant species in dung of cattle (*Bos taurus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and rabbits (*Oryctolagus cuniculus*). The mean seed density found in that study in cattle dung was 9.6/g of dry dung, similar to those found in bison dung in the present study. Myers et al. (2004) germinated seeds of 72 plant species from white-tailed deer (*Odocoileus virginianus*) pellets in eastern North America and Bakker & Olf (2003) germinated seeds from 35 plant species from cattle dung in floodplain grassland of the eastern Netherlands. Pakeman et al. (2002) found a high abundance and diversity of seeds dispersed by rabbits and sheep in eight sites in the United Kingdom.

Endozoochory by bison and other large ungulates has been successful in the dispersal of plant seeds, which lends support to Janzen's (1984) "foliage is the fruit" hypothesis. Gökbülak (2002) evaluated the feasibility of 'fecal seeding' by feeding bison seeds of six forages. Seed recovery from bison dung was greatest for round, hard seeds. Fecal seeding by cattle has been studied for *Panicum virgatum* (Ocumpaugh et al. 1996) and *Eragrostis lehmanniana* (Fredrickson et al. 1997), to establish pasture species (Malo & Suárez 1995b), and to restore richness in grasslands (Traba et al. 2003). Cosyns et al. (2005a) demonstrated tremendous potential for endozoochory by horses and cows to maintain plant diversity. Nevertheless, there are often large costs associated with endozoochory (especially strongly reduced germination after gut passage; Cosyns et al. 2005b), while seedling establishment after endozoochorous dispersal can be quite restricted (Cosyns et al. 2006).

We found several introduced species in bison dung, which indicates that bison can be important dispersers of such species. Myers et al. (2004) reported that 38% of species germinating from white-tailed deer (*Odocoileus virginianus*) pellets were non-native. How dispersal by bison affects plant abundance and distribution of introduced species is unknown, but represents a potentially important factor influencing vegetation dynamics in tallgrass prairie.

Seeds from any species may be dispersed by more than one means, even those with specialized modifications for a specific type of dispersal. Ridley (1930) described more than one mode of dispersal for a substantial number of plant species, and Lyons (1994) observed that seeds from *Desmodium* spp. were dispersed in a tallgrass prairie by other mechanisms beyond adhesion. Pakeman et al. (2002) observed that several wind-dispersed species were capable of being dispersed by endozoochory. In a study of donkeys, Couvreur et al. (2005a) found that endozoochory and epizoochory have complementary effects.

## Conclusions

In this study we document that bison hair and fecal pats contain a high abundance and diversity of plant seeds. Bison are thus potentially important dispersal agents of plant species in tallgrass prairie. Because seed richness and abundance were greater in cow hair than in bull hair or juvenile hair, our results also suggest that herd composition, which differs from historical herd composition (Rosas et al. 2005), might play an important role in vegetation. Moreover, our results have meaningful implications to application of disturbance including fire and grazing and their interaction within tallgrass prairie landscapes because of preferential patch selection by bison. However, as Zobel & Kalamees (2005) argue, the extent to which dispersal influences diversity remains a challenge to demonstrate. This study justifies additional work on bison seed dispersal in the tallgrass prairie by demonstrating that meaningful numbers and diversity of seeds are transported by bison through two mechanisms.

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