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Dispersal of Leafy Spurge (Euphorbia esula L.) Seeds in the Feces of Wildlife

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ABSTRACT.—Leafy spurge (*Euphorbia esula*) is an exotic, perennial, invasive weed in many areas of the northern United States and Canada. There are many instances in pastures and wildlands where individual or small clusters of leafy spurge plants are distant and upslope from larger patches, and wildlife have been suspected as seed dispersal agents. Wildlife can disperse seeds by ingestion then excretion of seeds in their feces. Fecal deposits of free-ranging deer (*Odocoileus hemionus* and *O. virginianus*; n = 176), sharp-tailed grouse (*Tympanuchus phasianellus*; n = 201) and wild turkeys (*Meleagris gallopavo*; n = 206) were collected during a summer in Theodore Roosevelt National Park (TRNP) in western North Dakota, and for deer only in Medicine Lake National Wildlife Refuge (MLNWR) in northeastern Montana. Feces were analyzed for the presence of leafy spurge seeds and any seeds found were tested for germinability and viability. Only one intact leafy spurge seed was found in one grouse fecal deposit and it was not viable. No leafy spurge seed was found in turkey feces. Two seeds that appeared to be immature leafy spurge seeds were found in one deer fecal deposit in TRNP, but neither seed was viable. One leafy spurge seed was found in each of four deer fecal deposits from MLNWR, but only one seed was viable and germinated. Seed-feeding trials with captive deer (n = 4), sharp-tailed grouse (n = 4) and wild turkeys (n = 4) were conducted to determine how leafy spurge seeds interact with the digestive systems of these animals. The only viable seeds defecated by grouse and turkeys were seeds excreted one day after ingestion. Two turkeys did not excrete any leafy spurge seeds and only a few viable seeds were defecated by the other two. One grouse defecated a larger number of viable seeds, but the other three grouse excreted only a few. Deer defecated viable seeds each of 4 d after ingesting them with most viable seed excreted on the first 2 d. These findings, along with those for the free-ranging animals, indicate that wild turkeys probably do not disperse leafy spurge seed while sharp-tailed grouse and deer may do so on a limited basis.

INTRODUCTION

Leafy spurge (*Euphorbia esula*) is a troublesome invasive plant in many areas of western North America. This perennial forb was introduced into North America from Eurasia in the 1800s (Hanson and Rudd, 1933). Its deep root system, vigorous root sprouting and aggressive growth enable it to spread rapidly and displace native vegetation (Belcher and Wilson, 1989).

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Leafy spurge is a major economic problem for land managers (Bangsund *et al.*, 1999). Leafy spurge reduces carrying capacity for some animals by decreasing forage production. Cattle and some wild ungulates [deer (*Odocoileus hemionus* and *O. virginianus*), elk (*Cervus elaphus*) and bison (*Bison bison*)] will totally, or partially, avoid areas that are heavily infested by leafy spurge (Lym and Kirby, 1987; Hein and Miller, 1992; Trammell and Butler, 1995).

Leafy spurge has several means of seed dispersal (Selleck *et al.*, 1962; Messersmith *et al.*, 1985). It can propel seeds away from the parent by the dehiscence of the seed capsule and seeds may also be dispersed via hydrochory (Selleck *et al.*, 1962). There is also limited evidence for animals dispersing its seeds (Noble, 1980; Blockstein *et al.*, 1987; Lacey *et al.*, 1992; Olson *et al.*, 1997), but there has been no investigation of the potential for wild ungulates to disperse leafy spurge via endozoochory. Selleck *et al.* (1962) suggested that deer might be vectors of leafy spurge seed, and deer are known to eat glade spurge (*Euphorbia purpurea*) in the eastern United States (Loeffler and Wegner, 2000).

The ability of birds to disseminate seed is also well documented (McAtee, 1947; Krefting and Roe, 1949; Howe, 1986; Dean *et al.*, 1990; Graham *et al.*, 1995; Ballard and Sytsma, 2000), but the role of birds as dispersers of leafy spurge seed has had little study. Several studies suggest that game birds could consume and disperse seed of *Euphorbia*. Stoddard (1946) reported that bobwhite quail (*Colinus virginianus*) utilized many members of the spurge family (Euphorbiaceae), including the genera *Tithymalus* and *Poinsettia* (both commonly included in the genus *Euphorbia*). Seeds of milky spurge (*Euphorbia* spp.) were found in the crops of two ring-necked pheasants (*Phasianus colchicus*; Severin, 1933). Seeds of *Euphorbia* spp. were also found in the crops of wild turkeys (*Meleagris gallopavo*) in Missouri (Schorger, 1966) and Arizona (Scott and Boeker, 1973). Noble (1980) reported that two leafy spurge seedlings grew from a sharp-tailed grouse (*Tympanuchus phasianellus*) dropping implicating these grouse as possible vectors. Mourning doves (*Zenaida macroura*) consume seeds of several species of the spurge family (Lewis, 1993) and have been suggested as a dispersal agent for leafy spurge seeds (Clute, 1937; Blockstein *et al.*, 1987).

Captive feeding studies have been conducted with domestic cattle, sheep and goats to determine their potential for dispersing weedy species (Atkeson *et al.*, 1934; Dore and Raymond, 1942; Burton and Andrews, 1948; Jones and Simao Neto, 1987; Gardener *et al.*, 1993). Feeding trials with leafy spurge seed are limited to domestic sheep and goats (Lacey *et al.*, 1992; Olson and Wallander, 2002) and mourning doves (Blockstein *et al.*, 1987).

In the northern Great Plains of North Dakota, leafy spurge spreads rapidly along drainages and other water corridors. For example, leafy spurge occupies about 1600 ha within the South Unit of Theodore Roosevelt National Park in western North Dakota, mostly along low-lying land, ephemeral creeks and rivers. However, leafy spurge has spread upstream and onto higher plateaus within this park with isolated populations appearing far from any obvious source. It is conceivable that wildlife may spread viable leafy spurge seeds in their feces to new locations, but no thorough investigations have been conducted.

Evidence from feeding trials has demonstrated that wildlife can consume and defecate viable seeds of various taxa (Krefting and Roe, 1949; Traveset, 1998). Even though deer and several game bird species can consume *Euphorbia* species, little evidence exists for utilization and dispersal of leafy spurge seeds by wildlife. The demand for research on leafy spurge seed dispersal by wildlife is propelled by its ecological and economic threat to public and private lands in North America. We determined whether deer (*Odocoileus hemionus* and

O. virginianus), sharp-tailed grouse and wild turkeys pass viable leafy spurge seed in their feces and therefore, can serve as dispersal agents.

METHODS

Study areas.—This study was conducted in Theodore Roosevelt National Park (TRNP) in western North Dakota (46°55′N/103°31′W) and at Medicine Lake National Wildlife Refuge (MLNWR) in northeastern Montana (48°29′N/104°27′W). The South Unit of TRNP consists of approximately 19,000 ha of non-glaciated terrain located in the Little Missouri Badlands (Bryce *et al.*, 1998). The area has an arid continental climate with a 10-y average (1991–2000) annual precipitation of 383 mm (NOAA, 2002). In the year when fieldwork for this study was done (2001), monthly precipitation for the important growing season months of May, June and July were 78% below, 46% above and 24% above the 10-y average, respectively. Vegetation has been described by Whitman (1979) and Hansen *et al.* (1984).

Medicine Lake National Wildlife Refuge consists of a large water body with several islands. The largest island ("Big Island") of approximately 100 ha was used in this study. Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), western snowberry (*Symphoricarpos occidentalis*) and leafy spurge dominated the vegetation on the island (Cooper and Heidel, 1999). This area has an arid continental climate with an average annual precipitation (1991–2000) of 355 mm (NOAA, 2002).

Leafy spurge utilization.—Observations were made to determine if wildlife were consuming leafy spurge. Four locations per study area with grazed spurge were sampled for utilization. Each location was sampled using a total of 100, 0.5 m^2 quadrats. We placed 25 m transects in the four cardinal directions radiating from the center of areas of grazed leafy spurge. Then we visually estimated the percent aerial cover and frequency of use of leafy spurge within 25 quadrats at one-meter intervals along each transect.

Fecal collection from free-ranging wildlife.—Areas where both the targeted wildlife species and leafy spurge infestations occurred were selected for fecal collections. Each area was searched at least once every 1 to 2 wk starting in late June. Number of samples collected each time varied depending on animal distribution within the area and the ability to find fecal deposits.

Managers of MLNWR observed browsing of leafy spurge on Big Island and suggested that white-tailed deer were responsible. Fecal samples were collected from the island on one occasion (12 July 2001) coinciding with peak production of mature leafy spurge seed on the island. We assumed that deer would consume seeds within seed capsules on plants and would be ineffective in picking seeds off the ground due to their small size.

Deer and turkey fecal samples from TRNP were collected 28 June to 24 August 2001 during leafy spurge seed maturation. Turkey samples were found mostly along a river corridor and in wooded draws. Deer samples from TRNP were collected from a greater variety of habitats (*e.g.,* river corridors, plateaus, wooded draws). Sharp-tailed grouse fecal samples were collected 2 August to 27 September 2001. They were collected at this time because we believed that grouse would consume more seeds at this time (Kobriger, 1965). We assumed grouse would consume leafy spurge seeds from the ground after the capsules dehisced because seed capsules on leafy spurge plants are typically out-of-reach for grouse; whereas turkeys could possibly select seeds before or after capsules dehisced. Grouse samples were mainly collected from grassy plateaus with clusters of shrubs.

Collecting fresh feces reduced the chances of rodent and insect predation of seeds within feces (Janzen, 1971; Janzen, 1982) and concentrated collection efforts to the specific periods when leafy spurge seeds were available to the target animals. Fresh feces were distinguished by characteristics of moistness and coloration.

Feces were examined to insure that no leafy spurge seeds from the soil surface contaminated the sample. Samples were stored frozen in plastic bags. Samples were later transferred to paper bags and dried in a forced-air drier at 35 C for 13 d to insure dehydration. Dried samples were stored at room temperature in paper bags within covered plastic storage containers until further processing.

Pen trials.—Four captive male deer (two white-tailed and two mule deer, weighing 69 to 136 kg and between 1.5 to 4.5 y of age) located at the South Dakota State University Wildlife Research Unit were used for the trial. Individual animals were separated into four, 2.5 m by 2.5 m pens with concrete flooring. The deer were accustomed to the pens from earlier studies so an extended adaptation period was unnecessary. Each animal was put into its pen one day before feeding leafy spurge seeds and given a ration of whole corn (*Zea mays*) and pelleted soybean (*Glycine max*) hulls. Dosage methods were similar to those described by Lacey *et al.* (1992). Deer were given 150 g pelleted soybean hulls mixed with 20 ml of molasses and top-dressed with 3000 (9.87 g) leafy spurge seeds. The average mass for 1000 leafy spurge seeds was 3.291 g. Lacey *et al.* (1992) also fed 3000 seeds to sheep with body weights similar to those of our deer. Each deer consumed the leafy spurge seeds within a couple of hours. All animals were given whole corn and water ad lib. for the remainder of the trial. Feces were collected for five consecutive days after dosing. All fecal samples were stored frozen until they were thawed and analyzed while still moist (Simao Neto *et al.*, 1987).

Four adult male sharp-tailed grouse were separated into individual 1.5- by 0.75- by 0.75 m cages with wire mesh floors to allow for passage of feces onto collecting trays. Grouse were acclimated after several days when birds readily consumed food and water and produced solid feces. During this period, the grouse were given game bird grower (Land O' Lakes Farmland Feed LLC, Fort Dodge, Iowa) and cracked corn along with grit (size #2) and water ad lib. Feed was withheld the previous evening to promote appetite the following morning before pulse dosing. The grouse did not ingest any seed when offered only leafy spurge seeds or a mixture of base food and leafy spurge seed. To pulse dose the grouse, we force fed each bird using a metal, v-shaped spatula to direct leafy spurge seeds into the esophagus. The mandibles were then held together until the bird swallowed the seeds. Each grouse was dosed with 4.936 g (about 1500 seeds by mass; volume = 5 ml) of leafy spurge seeds. Dosage size was based on Blockstein *et al.* (1987). After dosing, grouse were given access to grit, feed and water ad lib. Feces were collected daily for five consecutive days after dosing. Samples were analyzed fresh for seed content.

Four adult male turkeys were placed individually into cages of about 1 m^3 with wire mesh flooring to allow feces to drop through and onto collecting trays. Fabric was placed over the pens to keep the birds calm throughout the trial. The turkeys were relatively tame, but were not accustomed to confinement. Turkeys were allowed to acclimate to the pens for 7 d except for one replacement which was acclimated for 2 d. Birds were considered acclimated when they readily consumed food and water as well as produced solid feces. Each bird was given wheat screenings, water and grit (size #2) ad lib. Individual turkeys were pulse dosed 9.87 g (about 3000 seeds by mass; volume = 10 ml) of leafy spurge seeds using the force-feeding method described for grouse. Dosage of seeds was similar to that of grouse with adjustment for body size differences. Individuals had access to food, water and grit ad lib. for the rest of the trial. Fecal collections began the next day and ran for five consecutive days. Feces were analyzed fresh.

Recovery of seeds from feces.—Dried feces from free-ranging wildlife were presoaked in water for 30–60 min to soften and facilitate sieving (Jones and Bunch, 1988). Feces from free-ranging and feeding trial wildlife were analyzed following techniques described by Olson *et al.* (1997).

Each fecal sample was washed through a series of soil sieves with mesh sizes of 2 (#10), 1 #18) and 0.710 mm (#25). Samples were placed on the top sieve and rinsed with running water while lightly rubbing the material to promote the breakup of samples and to assist in the passage of finer material through the sieve. Material from sieves #10 and #18 was collected in the bottom sieve and back-flushed into an aluminum pie tin. The slurry was poured into a funnel lined with a coffee filter to separate water from the material. The material left on the filter was then analyzed for seed content under a dissecting microscope. All whole leafy spurge seeds within the sample were removed, dried and placed in glass scintillation vials and stored at room temperature. A whole seed was defined as one that was structurally intact, including seeds with fractures in the seed coat.

Testing of leafy spurge seeds.—Seeds found in feces were pre-chilled dry at 3 C for 14 d (Lacey *et al.*, 1992). Seeds were bathed in a 10% solution of chlorine bleach for 10 min and rinsed three times to help prevent fungal growth during germination (Olson and Wallander, 2002). Seeds were placed on three layers of #1 Whatman filter paper in 90 mm sterilized glass petri dishes. Deionized water was used to soak the filter paper and keep the seeds moist. Moisture content was checked and maintained with deionized water every 2 d until the trial was complete. Covered petri dishes were placed in a germinating chamber with alternating temperatures of 20 C for 16 h (dark) and 30 C for 8 h (with light) for 28 d (Selleck *et al.*, 1962). Seeds with radicles greater than 5 mm were counted as germinated and then removed. All non-germinated seeds were tested for viability by cutting the seeds and soaking them in 0.1% buffered (pH 7.12) sodium tetrazolium (TZ) at room temperature for 24 h. Embryos were examined under a dissecting microscope to determine viability by staining patterns (pink coloration) on the radicle and cotyledons (Grabe, 1970). Samples of leafy spurge seeds were collected from TRNP during July 2001 to serve as controls in germination trials. Data on leafy spurge seed found in feces that were collected in the field were not subjected to statistical analysis.

Statistical analyses of pen trial data.—Deer, turkey and grouse results were analyzed separately for differences in percent whole seeds recovered, percent germination and percent viability of seeds recovered, as well as percent seed survival of pulse-dosed seeds fed over the five-day collection period. Percent seed survival was calculated by dividing the number of viable seeds recovered by the initial number of viable seeds fed. We used PROC UNIVARIATE to test for normality (SAS, 1985). The Shapiro-Wilk test statistic was used to test the hypothesis of normal distribution (Zar, 1984). Percentage data were not normally distributed and were transformed using the arcsine square-root transformation method ($=\arcsin\sqrt{p}/100$, where p equals the original percentage value; Bartlett, 1947; Zar, 1984). For the deer trial only, PROC MIXED with the REPEATED statement was used to analyze day as the main effect and seed recovery, germination and viability as the response variables. Akaike's Information Criterion was used to determine the variance component with the best fit for the covariance structure. Multiple comparison tests of the least square means for each response variable were used to determine differences between days. Multiple comparisons were protected for experimentwise error rate by using $\acute{\alpha} = 1 - (1 - \alpha)^{1/k}$, where $\acute{\alpha}$= significant multiple comparison p-value, α = comparisonwise error rate (0.05), k = number of comparisons (Sokal and Rohlf, 1981). Most seeds from grouse and turkeys were obtained on the first day, so this test was not performed for them.

RESULTS

Leafy spurge utilization.—Within TRNP plots, 38% of quadrats containing leafy spurge had some degree of browsing of leafy spurge (*i.e.,* tops nipped off) by an herbivore. The aerial cover of leafy spurge within quadrats averaged 23 ± 1% (Table 1). Within MLNWR plots,

TABLE 1.—Leafy spurge utilization in plots in Theodore Roosevelt National Park (TRNP) and Medicine Lake National Wildlife Refuge (MLNWR). Each plot consisted of 100 0.5 m^2 quadrats. Numbers in parentheses are standard errors

Plot number	Number of quadrats with leafy spuge	Number of quadrats with utilization	Percent of leafy spurge quadrats with utilization	Average percent leafy spurge aerial cover within quadrats
TRNP-1	77	25	32	26.6 (± 5.4)
TRNP-2	73	26	36	28.4 (± 4.4)
TRNP-3	86	40	47	25.2 (± 6.6)
TRNP-4	49	18	37	15.6 (± 4.4)
Average	71	27	38	23.0 (± 1.3)[a]
MLNWR-1	88	45	51	14.6 (± 1.9)
MLNWR-2	68	25	37	6.8 (± 1.3)
MLNWR-3	88	27	31	43.2 (± 3.7)
MLNWR-4	70	25	36	28.2 (± 7.2)
Average	79	31	39	22.2 (± 1.2)[a]

[a] Quadrat averages were derived from all four plots (n = 400)

39% of quadrats that contained leafy spurge had utilization of leafy spurge by an herbivore. The aerial cover of leafy spurge within MLNWR quadrats averaged 22 ± 1% (Table 1).

Seed recovery from free-ranging wildlife.—Fecal samples from turkey (n = 206), sharp-tailed grouse (n = 201), TRNP deer (n = 134) and MLNWR deer (n = 42) were analyzed for leafy spurge seed content. No leafy spurge seeds were found in turkey feces. One intact *Euphorbia esula* seed was recovered from one grouse fecal sample collected in mid-August. The seed coat was scarified, indicating that the seed passed through the bird's digestive system. However, the seed was not viable. Two *Euphorbia serpyllifolia* seeds were recovered from one deer sample in late July, and two *Euphorbia* spp. seeds were recovered from another sample in late August; both samples were collected in TRNP. The *Euphorbia* spp. seeds appeared to be immature leafy spurge, but were not viable. One leafy spurge seed was found in each of four deer samples and two *Euphorbia* spp. seeds that appeared to be immature leafy spurge were recovered from another sample collected in mid-July from MLNWR. Only one leafy spurge seed was viable and germinated. All seeds had some degree of seed coat scarification indicating that the seeds passed through the digestive system of deer.

Feeding trial seed passage.—Recovery of whole leafy spurge seeds varied among individuals for each species (Table 2), and for deer they varied among days after ingestion (Table 3). Grouse passed a considerable number of seeds 1 d after ingestion (141 ± 83) and continued to pass some seeds through the third day. Of the 1500 seeds fed to grouse, the average recovery was 152 ± 87 seeds (10.1%). Turkeys only passed an average of 4 ± 3 seeds one day after ingestion and passed no seeds thereafter. No seeds were recovered from two of the turkeys. Over the 5-d trials, total seed recovery ranged from eight to 380 seeds per grouse and zero to 13 seeds per turkey. Viable seeds from these bird species were only recovered on the first day after ingestion.

Deer passed whole seeds all 5 d of the trial. The highest average number of seeds recovered from deer occurred 3 d after seed ingestion (33 ± 1) and declined thereafter (Table 3). Percent seed recovery data were different over the five days ($F = 22.21$, $P = 0.005$; Fig. 1). One deer passed no seeds on the first day.

Germination and viability of recovered seeds from pen trials.—The initial viability of seeds was 94% (deer were fed 2820 viable seeds). Percent germination and viability of seeds recovered

TABLE 2.—Numbers of seeds recovered from each individual of a species were summed over the 5-d feeding trial. Numbers of seeds that germinated, total seeds viable and percentage data are of recovered seeds. Grouse were fed 1500 seeds each; whereas, deer and turkeys were fed 3000 seeds each. Deer 1 and 2 were mule deer and individuals 3 and 4 were white-tailed deer. The control data are derived from replicates of 100 seeds with initial viability of 94%

Species	Individual	Seeds recovered (no.)	Seeds germinated (no.)	Germination (%)	Total seeds viable (no.)[a]	Total viability of seeds recovered (%)	Seed survival (%)[b]
Grouse	1	8	1	12.5	2	25.0	0.14
	2	380	16	4.2	60	15.8	4.25
	3	24	1	4.2	6	25.0	0.43
	4	196	0	0	4	2.0	0.28
Deer	1	205	10	4.9	23	11.2	0.82
	2	57	0	0	6	10.5	0.21
	3	92	6	6.5	15	16.3	0.53
	4	113	16	14.2	23	20.4	0.82
Turkey	1	0	0	0	0	0	0
	2	13	6	46.2	7	53.8	0.25
	3	0	0	0	0	0	0
	4	4	1	25.0	2	50.0	0.07
Control	1	—	—	93.0	—	96.0	—
	2	—	—	85.0	—	92.0	—
	3	—	—	94.0	—	97.0	—
	4	—	—	72.0	—	94.0	—
	5	—	—	90.0	—	96.0	—
	6	—	—	64.0	—	89.0	—

[a] Total seeds viable include seeds that germinated and seeds that tested positive with tetrazolium

[b] Percent seed survival is derived by dividing total seeds viable by the number of seeds initially viable (1410 of 1500 and 2820 of 3000)

from the birds declined with the number of days of retention in the gastrointestinal tract (Table 3). The only seeds that germinated (or were viable) from grouse and turkey samples were those passed one day after ingestion (Table 3).

Seeds passed by deer germinated irrespective of time spent in the gastrointestinal tract ($F = 0.87$, $P = 0.47$; Fig. 2). Deer passed viable seeds for four consecutive days after ingestion. The average viability of recovered seeds was the greatest at 2 d after seed ingestion (49 ± 9%), and subsequently decreased to 1.3 ± 1.3% at 4 d. Seed viability was lower after day two ($F = 14.89$, $P = 0.009$; Fig. 3).

Survival of seeds initially fed was low for each species. Leafy spurge seed survival over the five-day trial was 1.3 ± 1% for grouse, and 0.08 ± 0.06% for turkeys. Survival of seeds ingested by deer was 0.6 ± 0.1% over the 5-d trial. The seed survival data from deer indicated a decrease in seed survival after day two ($F = 10.92$, $P = 0.007$; Fig. 4).

DISCUSSION

Leafy spurge utilization by wildlife.—Grazing of leafy spurge by wildlife has not been reported; however, several infestations of leafy spurge within TRNP and MLNWR showed signs of browsing by wildlife. We assume that deer may have eaten leafy spurge at TRNP since analysis of deer feces from MLNWR indicated that they ate it there. The observed utilization on leafy spurge in TRNP was rather high on the plants and did not exhibit the

TABLE 3.—Number of leafy spurge seeds recovered, percent germination and percent viability of seeds recovered from grouse, deer and turkeys on subsequent days after ingestion. Percent viability included seeds that germinated and that tested positive with tetrazolium. Each grouse was fed 1500 seeds. Each deer and turkey was fed 3000 seeds

Species	Days after ingestion	Seeds recovered (no.)	Germination (%)	Viability (%)[a]	Seed survival (%)[b]
Grouse	1	140.75 ± 82.95	14.70 ± 11.81	36.25 ± 21.81	1.28 ± 0.99
	2	10.25 ± 4.27	0	0	0
	3	1.00 ± 0.41	0	0	0
	4	0	0	0	0
	5	0	0	0	0
Deer	1	2.25 ± 1.31	16.67 ± 11.79	41.67 ± 22.05	0.03 ± 0.01
	2	32.00 ± 11.68	14.49 ± 5.05	48.70 ± 8.99	0.45 ± 0.14
	3	33.25 ± 1.03	4.74 ± 3.00	9.21 ± 2.33	0.11 ± 0.02
	4	19.00 ± 3.63	0	1.32 ± 1.32	0.01 ± 0.01
	5	30.25 ± 18.61	0	0	0
Turkey	1	4.25 ± 3.07	17.79 ± 11.14	25.96 ± 15.01	0.08 ± .06
	2	0	0	0	0
	3	0	0	0	0
	4	0	0	0	0
	5	0	0	0	0
Control	—	—	83 ± 5.02	94 ± 1.24	—

[a] Percent viability includes seeds that germinated and seeds that tested positive with tetrazolium

[b] Percent seed survival is derived by dividing total viable seeds recovered by the number of seeds initially viable

characteristic angled cut created by incisors to suggest that rodents or rabbits had grazed it. However, we can not rule out the possibility that some other herbivore besides deer grazed it. Elk, bison and feral horses (*Equs caballus*) also occur in the park. Given that the diet of bison and horses consists mainly of graminoids and the feces of deer and elk were commonly found in the area where utilized leafy spurge was observed, we suspect that one or both of these latter ungulates grazed leafy spurge.

Seed recovery from free-ranging wildlife.—Wild turkeys inhabit woodlands along the Little Missouri River and other wooded draws within TRNP. Several areas within TRNP where turkeys were abundant were infested with leafy spurge and its seed is readily available to turkeys. However, no leafy spurge seeds or even seed fragments were identified from the 206 samples analyzed from field collections. Turkeys consume flowers, leaves, and fruits of *Euphorbia nutans* (Schorger, 1966) and other *Euphorbia* species (Scott and Boeker, 1973), but consumption of leafy spurge by turkeys is not reported. If they do eat them, they do not survive gut passage. Our data indicate that wild turkeys within TRNP are not vectors of leafy spurge seed.

Sharp-tailed grouse inhabit areas within TRNP where leafy spurge appears sporadically under patches of sagebrush (*Artemesia* spp.), chokecherry (*Prunus virginiana*), buffaloberry (*Shepherdia canadensis*) and skunkbush sumac (*Rhus trilobata*). Nearly all grouse fecal samples were collected in these habitats, especially from roost sites under sagebrush. Grouse within these areas had the potential to consume leafy spurge capsules as well as seed from the ground. One intact leafy spurge seed was recovered from one grouse fecal sample, indicating the possibility of dispersal by grouse. The recovery of only one nonviable seed from 201 fecal samples indicates that grouse may not selectively consume leafy spurge seeds within TRNP at

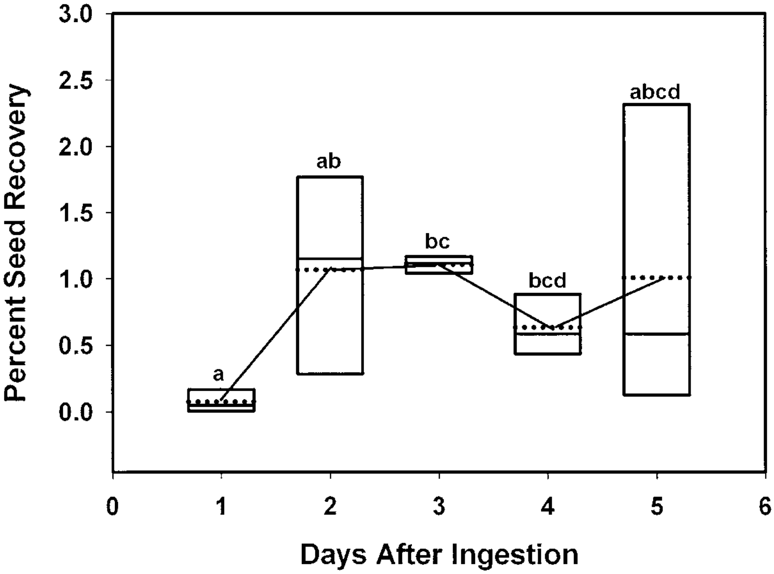

FIG. 1.—Untransformed percent seed recovery of leafy spurge seeds ingested by deer during a 5 d trial. Different letters represent a significant difference protected for experimentwise error. The boundary of the box closest to zero indicates the 25th percentile, a solid line within the box marks the median, a dotted line within the box represents the mean, and the boundary of the box farthest from zero indicates the 75th percentile

least during years with good summer precipitation and seed production by many plant species as was the case during the summer of fieldwork for this study. Since leafy spurge is tolerant of drought and can produce seed in dry years, its seed could be relatively more abundant and perhaps utilized more by grouse in dry years (Mitchell and Riegert, 1994). Noble (1980) reported that two leafy spurge seeds germinated from a wild sharp-tailed grouse fecal deposit suggesting that free-ranging grouse can disperse viable leafy spurge seeds within feces.

White-tailed deer primarily inhabit wooded corridors along the Little Missouri River and its major tributaries; whereas, mule deer inhabit most other habitats (*e.g.*, wooded draws, sagebrush communities, buttes and wooded slopes) within TRNP. Leafy spurge occurs in most habitats with varying degrees of abundance, as do deer. Deer had the potential to consume leafy spurge and its seed capsules within these habitats. The timing of consumption of viable seeds would have to coincide with the maturation of the seeds before the capsules dehisced. The duration of time when leafy spurge seeds were mature and viable to when capsules dehisced was about two weeks, depending on ambient temperature. This period is relatively short, but leafy spurge inflorescences do not mature or release seeds synchronously. Many microclimates within TRNP can affect maturation of leafy spurge. Seed maturation occurred from late June through September, with the majority of spurge seed ripening in July and August. Collecting deer samples from late June through August coincided with leafy spurge maturation and increased chances of recovering seeds within feces. Deer consumed and passed some *Euphorbia* seeds within TRNP. Two *E. serpyllifolia* and two immature *Euphorbia* spp. seeds were recovered from 134 deer samples.

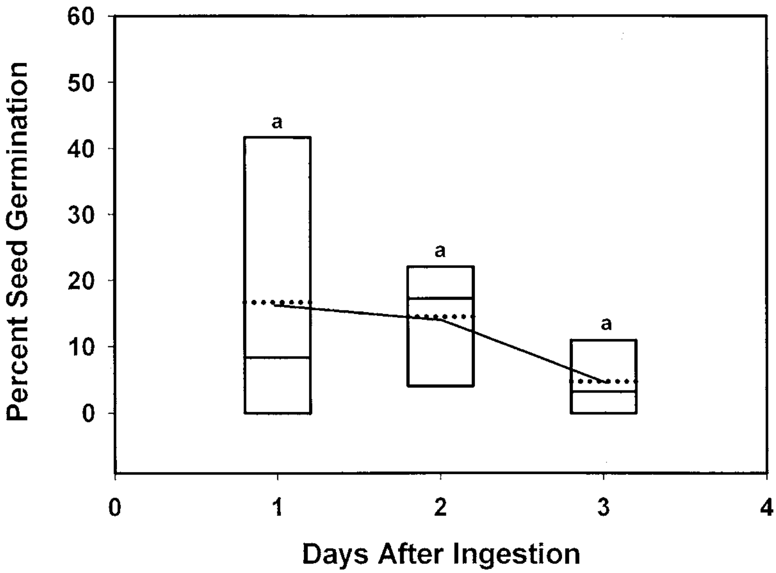

FIG. 2.—Untransformed percent seed germination of leafy spurge seeds recovered from deer after ingestion. Different letters represent a significant difference protected for experimentwise error. The boundary of the box closest to zero indicates the 25th percentile, a solid line within the box marks the median, a dotted line within the box represents the mean, and the boundary of the box farthest from zero indicates the 75th percentile

Deer use Big Island of MLNWR as a sanctuary to reduce predation and other disturbances especially during fawning. Although deer can swim between the mainland and island daily, they may not leave the island as often when they have fawns. The difference in leafy spurge seed recovery in TRNP vs. MLNWR may reflect differences of total area, vegetative composition and deer densities between study areas. The search area in TRNP was much greater than it was for MLNWR, increasing the likelihood of not finding fecal samples or not finding samples with leafy spurge seeds. Forty-two deer samples were collected at MLNWR in 1 d, whereas it took several weeks to collect 134 samples in TRNP. Vegetation in TRNP is more diverse than on Big Island of MLNWR. Deer living on the island have a reduced selection of forage compared to TRNP deer. The greater density of deer and leafy spurge on Big Island likely increased the chance of finding leafy spurge seeds in deer feces.

Feeding trials—grouse and turkey.—In this study, the total number of leafy spurge seeds recovered varied between species. Viable seed recovery was, however, very low for both grouse and turkeys. Comparative feeding studies using gallinaceous birds are limited. Krefting and Roe (1949) could not determine recovery rates of wild rose (*Rosa* spp.) seeds collected from wild grouse droppings, but they did show that germination rate increased after ingestion compared to seeds collected from nearby shrubs. Harmon and Keim (1934) found chickens to pass 1.2% viable velvet-leaf (*Abutilon theophrasti*) seeds of those ingested; whereas, Swank (1944) found that pheasants passed 3% of millet (*Panicum miliaceum*) and 5% of red clover (*Trifolium pretense*) as viable seeds.

Most seedeaters depend more on their gizzard than their proventriculus for digestion, which could affect seed passage depending on the size of gizzards (Gill, 1995). Since a turkey's gizzard can crush pecan nuts within 1 h and a hickory nut within 31 h (Schorger,

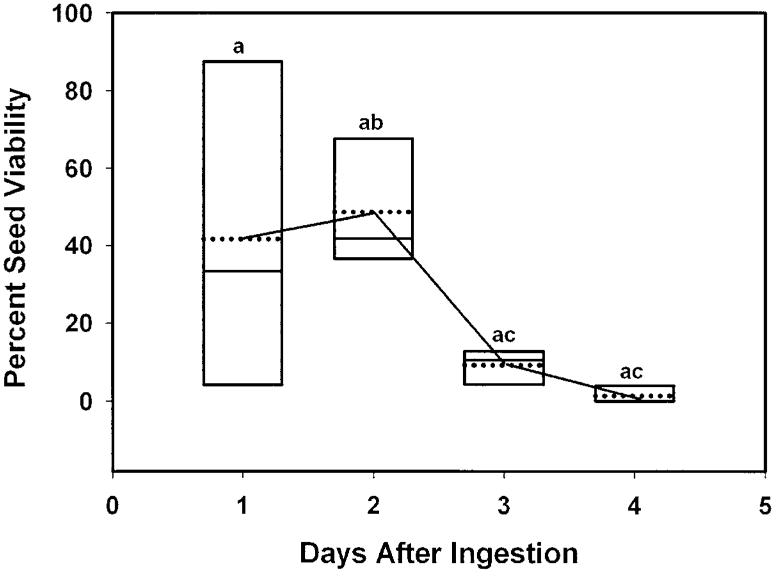

FIG. 3.—Untransformed percent seed viability of leafy spurge seeds recovered from deer after ingestion. Different letters represent a significant difference protected for experimentwise error. The boundary of the box closest to zero indicates the 25th percentile, a solid line within the box marks the median, a dotted line within the box represents the mean, and the boundary of the box farthest from zero indicates the 75th percentile

1960), it is no surprise that very few leafy spurge seeds were recovered from turkeys. Grouse have a smaller gizzard than turkeys do, so grouse may pass more spurge seeds than turkeys do. However, Blockstein *et al.* (1987) found that 6-month-old mourning doves (with an even smaller gizzard than grouse) destroyed ingested leafy spurge seeds. Krefting and Roe (1949) found that pheasants destroyed more (100%) smooth sumac (*Rhus glabra*) seeds than quail did (65%); however, the smaller gizzard of quail destroyed more hawthorn (*Crataegus* spp.; 25%) seeds than did pheasant gizzards (0%). The above discussion clearly indicates contradictions relating gizzard size to seed passage and may indicate that seed physiology and/or gizzard content (*i.e.*, grit) have greater influences on seed passage.

Feeding trials—deer.—Similar variations in seed recovery and viability have been observed in ruminants. Recovery of leafy spurge seeds from deer over the 5-d trial ranged from 57–205 seeds per deer. Piggin (1978) observed a similar range of seed recovery (41–275) from sheep that were grazing *Echium plantagineum.* Of the 3000 leafy spurge seeds fed to each deer, the average recovery was 116.75 ± 31.60 seeds (3.89%) over the 5 d; however, the deer were still passing seeds on the last day of the trial. Comparable to our study, Olson and Wallander (2002) found that the greatest recovery of leafy spurge seed from sheep was about 4%. However, Lacey *et al.* (1992) reported that total leafy spurge seed recovered from both sheep and goats was 18% of the seeds fed. Wallander *et al.* (1995) also recovered about 4% of spotted knapweed (*Centaurea maculosa*) seed fed to sheep, but recovered 11% from mule deer over a 10-d trial during which deer were still passing seed through the last day. Lacey *et al.* (1992) found that most leafy spurge seeds were passed within the first three days after ingestion by goats; however, they found that sheep continued to pass spurge seeds 9 d after ingestion. In our study, seed passage was highest on days 2 and 3 after ingestion.

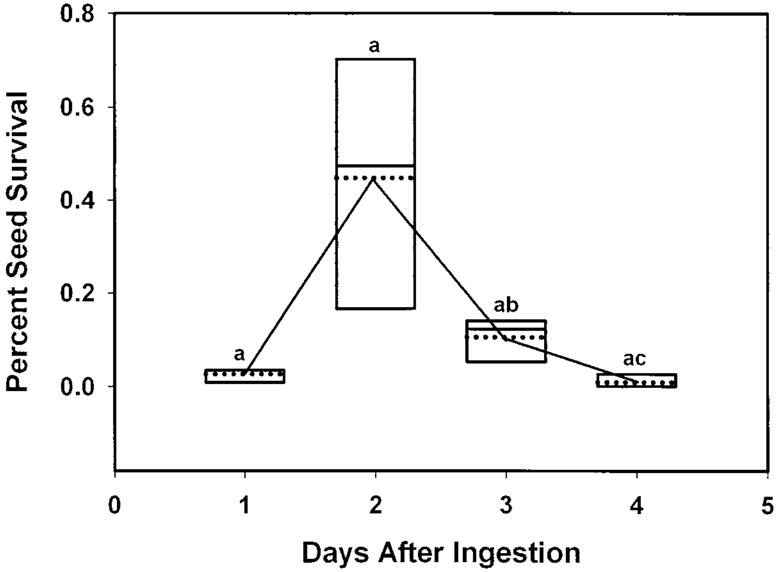

FIG. 4.—Untransformed percent seed survival of leafy spurge seeds initially fed to deer. Different letters represent a significant difference protected for experimentwise error. The boundary of the box closest to zero indicates the 25th percentile, a solid line within the box marks the median, a dotted line within the box represents the mean, and the boundary of the box farthest from zero indicates the 75th percentile

Comparably, Olson and Wallander (2002) reported that recovery of mature leafy spurge seeds from sheep was the highest 2 d after ingestion and declined through day 5 at the end of the trial. Several other feeding studies indicate similarly high variability in other herbivores (*e.g.,* Burton and Andrews, 1948; Heady, 1954; Lehrer and Tisdale, 1956; Janzen, 1981*a, b*; Janzen, 1982; Gardener *et al.*, 1993) even within the same individuals (Mautz and Petrides, 1971).

Deer passed viable seeds only through day 4, and viability decreased with longer retention times. Olson and Wallander (2002) also showed viable leafy spurge seeds passing up to 4 d after ingestion by sheep and viability declining with longer residence time. Several other studies have shown that seed viability decreases as residence time in the digestive tract increases (Simao Neto and Jones, 1987; Gardener *et al.*, 1993; Ocumpaugh and Swakon, 1993). Of the total seeds recovered from deer over the 5-d trial, viability (germination plus positive TZ) was only 14% compared to 94% for controls. Similarly, Lacey *et al.* (1992) found sheep and goats to pass viable leafy spurge seeds up to 4 d after ingestion, with viability reduced from 90% to 14% and 31%, respectively.

Physical structure and quality of forage can affect the passage rate of digesta (Welch and Hooper, 1988; Ortmann *et al.*, 1998) and subsequent recovery of ingested seeds (Ocumpaugh and Swakon, 1993). Jones and Simao Neto (1987) reported that sheep passed more seeds, and at a faster rate, with a high quality diet. Mautz and Petrides (1971) also reported that non-processed foods such as aspen leaves, sumac inflorescences and grass clippings had a mean retention time about 30% longer than forage in a concentrated pellet form. In our study, we pulse-dosed deer with 150 g of pelleted soybean hulls and offered whole corn ad lib. This may have caused a faster passage rate and elevated seed viability compared to deer on a natural diet consisting of more browse. However, we believe that during the time of year when leafy spurge seed is available to deer, high quality foods are also available, which increase passage rates. Therefore, we feel that passage rates were probably similar between our feeding trial deer and wild deer consuming high quality forage.

CONCLUSIONS AND RECOMMENDATIONS

This study suggests that deer, sharp-tailed grouse and wild turkeys are not major endozoochorous vectors of leafy spurge. Our feeding trial and field data indicate that survival of ingested seed through the gastrointestinal tract is low to very low and leafy spurge seed was seldom found in the feces of these animals. If endozoochoric dispersal of leafy spurge was common, then long distance dispersal of leafy spurge in TRNP would likely be more pronounced because these animal species and leafy spurge have interacted there for decades. Our results indicate that grouse and deer could possibly disperse low numbers of viable leafy spurge seeds in the wild; whereas, turkeys are not likely to serve as vectors at all. Admittedly, only one viable leafy spurge seed is required to initiate an infestation, but endozoochoric dispersal of viable seed by deer or grouse appears to be a low probability event.

Other possible long-distance dispersal agents of leafy spurge seed should be investigated. Seed caching by rodents is an important mode of dispersal for seeds of many plants and could be a plausible mechanism for leafy spurge, although probably not over long distances. Additionally, seed-eating songbirds could disperse leafy spurge seed, and feeding trials using grassland birds should be conducted to gauge this possibility. Ectozoochoric methods of leafy spurge seed dispersal should also be studied. For example, bison hair has characteristics similar to sheep wool and could possibly pick up seeds while bison roll on the ground dusting themselves. Seeds could then be dispersed when their hair is rubbed or shed. Many of the leafy spurge infestations in TRNP are near water sources used by wildlife. It is possible that animals could collect mud that contains leafy spurge seeds on their feet and then transport the seeds to new areas. Until these possibilities are studied, wildlife cannot be discounted as important dispersal agents for this invasive plant.

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