PLANT ANIMAL INTERACTIONS

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Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America

Abstract For many plant species in eastern North America, short observed seed dispersal distances (ranging up to a few tens of meters) fail to explain rapid rates of invasion and migration. This discrepancy points to a substantial gap in our knowledge of the mechanisms by which seeds are dispersed long distances. We investigated the potential for white-tailed deer (*Odocoileus virginianus* Zimm.), the dominant large herbivore in much of eastern North America, to disperse seeds via endozoochory. This is the first comprehensive study of seed dispersal by white-tailed deer, despite a vast body of research on other aspects of their ecology. More than 70 plant species germinated from deer feces collected over a 1-year period in central New York State, USA. Viable seeds included native and alien herbs, shrubs, and trees, including several invasive introduced species, from the full range of habitat types in the local flora. A mean of >30 seeds germinated per fecal pellet group, and seeds were dispersed during all months of the year. A wide variety of presumed dispersal modes were represented (endo- and exozoochory, wind, ballistic, ant, and unassisted). The majority were species with small-seeded fruits having no obvious adaptations for dispersal, underscoring the difficulty of inferring dispersal ability from diaspore morphology. Due to their broad diet, wide-ranging movements, and relatively long gut retention times, white-tailed deer have tremendous potential for effecting long-distance seed dispersal via ingestion and defecation. We conclude that white-tailed deer represent a significant and previously unappreciated vector of seed dispersal across the North American landscape, probably contributing an important long-distance component to the seed shadows of hundreds of plant species, and providing a mechanism to help explain rapid rates of plant migration.

Keywords Dung · Endozoochory · Herbivore · Invasive species · *Odocoileus virginianus*

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Introduction

Long-distance seed dispersal is currently of intense interest, because of its critical importance for invasion dynamics, population structure, and vegetation response to climate and land-use changes (Pitelka 1997; Cain et al. 2000; Bullock et al. 2002). Environmental change, whether natural or anthropogenic, is constantly altering local habitat conditions that influence demographic processes in plants. When previously unsuitable habitat conditions become suitable for establishment, successful colonization depends on dispersal of seeds into the altered habitat. If there are no nearby seed sources, "long-distance" dispersal is essential (i.e., >100 m; Cain et al. 2000). The dynamics of metapopulations and genetic structure, especially in fragmented habitats, and rates of plant migration (post-glacial and otherwise), are also strongly influenced by long-distance movements.

Despite the disproportionate effect of long-distance dispersal on a host of ecological and evolutionary processes, rare long-distance seed dispersal events are difficult to document (Cain et al. 2000), and dispersal ability and vectors are frequently inferred from diaspore type (e.g., Willson 1993; Cain et al. 1998). Several groups of species have generally been considered to lack long-distance dispersal ability, including seeds dispersed by ants or ballistically, as well as diaspores with no obvious morphological adaptations for a particular mode of dispersal, sometimes called "unassisted" (Willson 1993; Hughes et al. 1994; Cain et al. 1998). However, several observations suggest that long-distance movement is

achieved in ways other than the presumed dispersal mode. Forest herb species considered to lack long-distance dispersal have colonized successional stands isolated from potential seed sources (Matlack 1994; Grashof-Bokdam and Geertsema 1998), and variation among species in colonization rate into successional forests is often not directly related to diaspore type (Singleton et al. 2001; Verheyen et al. 2003; Flinn and Marks 2004). Given the advantages of dispersal, another apparent anomaly is the large number of species considered to have no special seed dispersal morphology, accounting for 20–50% of the plant species in some regions (Willson et al. 1990; Willson 1993). Finally, the rates of post-glacial migration that have brought many herbaceous plants to their current distributions appear to be much more rapid than can be explained by empirical observations of seed dispersal by these species (Cain et al. 1998). Despite many years of research on seed dispersal (Ridley 1930; Murray 1986; Bullock et al. 2002), these inconsistencies reveal significant gaps in our knowledge of how seeds move long distances.

Large grazing mammals have long been recognized as potentially important seed dispersers (Ridley 1930). Domestic cattle and sheep can deposit vast quantities of pasture plant seeds in their dung (Dore and Raymond 1942; Welch 1985), but wild ungulate species that range more widely have much greater potential for long-distance seed dispersal. Viable seeds can be abundant in the feces of wild ungulates (Ridley 1930; Malo et al. 2000; Heinken et al. 2002), especially those from species with small or hard-coated seeds. Janzen (1984) suggested that species with traits such as edible foliage and small hard seeds, retained on the plant, may in fact be adapted for seed dispersal by large herbivores. However, endozoochorous dispersal by herbivores is not limited to small-seeded species (Pakeman et al. 2002), and for most plant species it remains unknown whether viable seeds are actually dispersed this way. To the degree that wild ungulates in different regions may disperse a variety of diaspore types, including species considered to have "unassisted" dispersal, this could provide a general mechanism to help explain some of the apparent inconsistencies in the dispersal literature described above.

The dominant large wild herbivore throughout much of eastern North America is the white-tailed deer (*Odocoileus virginianus* Zimm.), which forages in a variety of habitats, including forests, fields, and suburban yards. White-tails are medium-sized deer (±40–100 kg), whose range extends from southern Canada to South America (Halls 1984). Where densities of white-tailed deer are high, there is widespread concern about the major negative impacts of deer herbivory on tree regeneration, forest herbs, prairie natives, crops, and ornamentals (Sayre et al. 1992; Anderson et al. 2001; Rooney 2001; Tzilkowski et al. 2002). Given their economic importance as a game resource, there is a vast body of research on most aspects of the ecology of white-tailed deer, including feeding preferences and movement patterns (see Halls 1984; Vellend et al. 2003). It is thus surprising how little is known about their potential as seed dispersers. Current information is limited to reports of germinable seeds of one or two species in feces of white-tailed deer (Gonzalez-Espinosa and Quintana-Ascencio 1986; Kramp et al. 1998; Campbell and Gibson 2001), or with viable seeds not distinguished from damaged remains (Lay 1965). We have recently demonstrated the potential for seed dispersal by white-tailed deer to contribute to the invasive spread of *Lonicera* honeysuckles (Vellend 2002), and to the post-glacial migration of *Trillium grandiflorum*, an ant-dispersed forest herb (Vellend et al. 2003). Deer travel across a home range of many hectares each day, and a seed shadow modeled from white-tailed deer movement patterns and gut retention times indicates that 95% of the seeds that are successfully dispersed would be carried >100 m, and 30% would be taken farther than 1 km (Vellend et al. 2003).

We hypothesized that white-tailed deer are a significant vector of seed dispersal, which potentially could help explain relatively rapid rates of plant colonization and migration in eastern North America. To test this, we conducted the first detailed survey of the plant species dispersed via endozoochory by white-tailed deer. We quantified the abundance and taxonomic diversity of viable seeds from deer feces collected over a full year, and the range of ecological characteristics (habitat affinity, presumed seed dispersal mode, etc.) of the germinating species. White-tailed deer feces were collected from two sites in central New York, USA, in a landscape representative of much of eastern North America: a mosaic of forest stands, active agriculture, old fields, and suburban development.

Materials and methods

Study sites

White-tailed deer feces, which are deposited as "pellet groups," were collected in 2000–2001 from two mixed deciduous forests in Ithaca, in the Finger Lakes region of New York State, USA. The first site, McGowan's Woods (76°27′2″W, 42°26′44″N), is a 10 ha forest bordered by agricultural fields, old field, roadside, and residential lawn, with a nearby creek and associated riparian vegetation. Our focus on forests stemmed from an initial interest in the role of deer in dispersing seeds of *Trillium* (Vellend et al. 2003) and potentially other forest herbs. It was soon apparent that the deer feces contained seeds of many species from the surrounding landscape, so we broadened the study to assess the role of deer in dispersing species of a range of habitats in our region. A second, larger forest stand (Six-mile Creek) was added in 2001, to enhance the likelihood of finding forest herb seeds. At Six-mile Creek (76°27′42″W, 42°25′55″N; 2.5 km from McGowan's Wood), deer feces were collected from a 3 ha portion of the woods at the Mulholland Wildflower Preserve, which is within a 70 ha strip of forest along the creek, bordered by suburban development and a few fields. The land in the vicinity of Six-mile Creek (based on aerial photographs, within a 1-km-radius circle centered on the collection area) is 44% forested and 2% fields; the other 54% is primarily residential, including yards and other landscaped areas, roadsides, etc. In contrast, the area within 1 km of the McGowan's site is only 25% forested, with 45% in agricultural fields, and 30% other.

Pellet group samples

Collections of white-tailed deer feces were made approximately semi-monthly at McGowan's Woods from October 2000 through September 2001, for a total of 97 pellet groups (2–6 on each of 23 dates). At Six-mile Creek Woods, pellet groups were collected semi-monthly from May through September 2001 (3–5 on each of nine dates; 37 total pellet groups). We sampled along widely-separated transects across each site, and care was taken to collect only entire, recently-deposited pellet groups, removing any surface material that might contaminate the sample with seeds. The collected pellet groups were 18±9 g dry mass (mean±standard deviation).

To determine the number of germinable seeds in each pellet group, we provided conditions likely to promote germination of many species. To facilitate species identification from seed characteristics, we examined half of each pellet group for seeds, by rinsing the material in a 0.5 mm sieve and sorting through the sample under magnification. The seeds found, and all residual fecal material from the sieve, were placed (separately) on moistened filter paper in petri dishes for moist, cold stratification (3 months at 4°C). In addition, to allow as wide a variety of species as possible to germinate, the other half of each pellet group was air-dried at room temperature for 10 days before dry cold stratification, for the same 3-month period. Following stratification, the pellet material and seed dishes were moved to warm conditions, and germination was monitored for 4 months. Pellet material was spread onto the surface of soil-less potting mix in individual pots, and kept moist. To keep germination conditions constant for pellet groups collected over the full year, we put seed dishes and the pots of McGowan's samples into a growth chamber with daily light/dark cycles at 25°/15°C; due to space constraints, Six-mile Creek pots were kept in a greenhouse (ca. 26°C). Germination from the two halves of each pellet group (moist vs dry stratification) was highly correlated ($r=0.97$, $P<0.0001$), and the median difference between halves was <1 germinable seed. Therefore, we report the total number of germinable seeds for entire pellet groups. Seedlings from the dishes and pots were kept until they could be identified to species: some had diagnostic seed and leaf characters, but most species were transplanted and grown until flowering to verify identification.

Additional data on species dispersed

We also report here the species that germinated from an initial set of samples, collected from McGowan's Woods to study dispersal of *Lonicera* and *Trillium* (Vellend 2002; Vellend et al. 2003) during 3 weeks of their fruiting period in summer 2000 (33 pellet groups; 20 July to 12 August). For these pellet groups, seeds >2 mm were retrieved for germination in petri dishes, seeds and residual pellet material were given 4 months of moist cold stratification, subsamples of residual material were spread onto potting mix for germination of small-seeded species, and germination from seed dishes and pots was monitored in the growth chamber for 4 months. Data from these samples are included in an overall summary of the traits of species dispersed by white-tailed deer at the two study sites, but because of the short sampling period and some differences in methods, for simplicity we do not present quantitative data from this preliminary collection.

Data analysis

For the samples from the full-year collection at McGowan's Woods, and the 5-month period at Six-mile Creek, we present the total numbers of germinations and species, and the median and maximum values per pellet group over the sampling period, and by month. Since seed availability varies across the seasons, to express the overall mean number of germinations per pellet group at each site, we averaged the monthly means, thereby adjusting for variation in sample number among months. For the number of species per pellet group (richness), we counted occasional seedlings that died before they could be identified only if differentiable from all other taxa in the sample. For simplicity we refer to all taxa as species. We also report, for each of the species, the numbers of germinations and the frequency of pellet groups in which the species occurred.

To present an overall summary of traits of the germinating species, we categorized them by growth habit, habitat, origin (native; introduced; or mixed, i.e., species with plants of both native and non-native origin here in the northeast), dispersal type, and seed size (see Electronic Supplementary Material for details), excluding unidentified taxa (2% of all germinations). This species trait summary is based on all data: the McGowan's full-year samples, the Six-mile Creek collection (May–September), and the initial set of McGowan's samples from July–August 2000. For calculating the contribution of each species to overall germination, we used the annual mean number of germinations per pellet group, averaged from the 12 monthly means for each of the species, to avoid biasing for species dispersed in summer months in this pooled set of data.

Results

More than two-thirds of the fecal pellet groups of white-tailed deer contained germinable seeds, at both McGowan's Woods and Six-mile Creek, for a total of >3,000 germinations (Table 1). Averaged over the full year at McGowan's Woods, there were 38 germinable seeds per pellet group. The number of germinable species in each pellet group was generally low (medians of 1), with a maximum of 11 species (Table 1). Overall, at least 72 species germinated, including forbs, grasses and sedges,

Table 1 Germinable seeds in white-tailed deer feces collected from two sites in Ithaca, New York: McGowan's Woods (97 pellet groups; October 2000–September 2001), and Six-mile Creek Woods (37 pellet groups; May–September 2001)

	McGowan's (full year)	Six-mile Creek (May–September)
Percentage of pellet groups with germinable seeds	67	68
Number of germinated seeds	3,431	217
Seed density (germinations per pellet group)		
Median	3	1
Maximum	1,985	52
Overall mean germinations per pellet group (average of monthly means)	38	5.3
Species richness per pellet group		
Median	1	1
Maximum	11	5
Total number of germinating species	57	21

shrubs, and trees (Table 2). The full-year samples from McGowan's had 57 germinable species, many of which were also in the Six-mile Creek samples, which had a total of 21 species. An additional ten species germinated only in the initial set of McGowan's samples from summer 2000 (Table 2). Most species were relatively uncommon (<10 seeds total), and many occurred in only one pellet group (Table 2). There were also seeds of at least four taxa that appeared viable but did not germinate (listed in square brackets in Table 2, with the symbol †).

The species with by far the most germinations was *Chenopodium glaucum* (Table 2), an annual roadside weed of European origin, with several pellet groups each having >100 seeds of that species. *C. glaucum* was in 12% of the full-year samples at McGowan's Woods (Table 2), and was also abundant in the McGowan's pellet groups from summer 2000, but was not present in the Six-mile Creek samples. The next most numerous species at McGowan's (Table 2) were: *Lythrum salicaria*, an invasive wetland plant; *Potentilla norvegica*, a weed of cultivated fields that is both native and introduced in North America; and *C. album*, another agricultural weed from Europe. Seeds of invasive *Lonicera* shrubs (*L. morrowii*, *L. tatarica*, and their hybrid *L. ×bella*; see Vellend 2002) were among the most abundant taxa at both sites, especially Six-mile Creek. Most other species in the Six-mile Creek pellet groups were found in low numbers (Table 2). The most abundant species at McGowan's did not have the highest relative frequency; *Plantago major* and *Juncus tenuis* germinated from the greatest number of pellet groups (Table 2). Both are weeds of lawns and paths: *J. tenuis* is native to North America and *P. major* is naturalized.

The species germinating from white-tailed deer pellet groups at the two sites encompassed a wide range of morphological and ecological characteristics (Table 3; Electronic Supplementary Material). Of the 72 identifiable taxa that germinated (Table 2), most (61%; Table 3, a) were forbs (non-graminoid herbaceous plants), and 39% of the 72 were annuals (Electronic Supplementary Material). The majority of species (81%) were taxa of open habitats (e.g., agricultural fields, old fields, roadsides). However, there were also five wetland and five forest species, and several of mixed habitat (Table 3, b). Many of the species (64%) are not native to northeastern USA. The overall number of germinations was dominated by forbs (90% of germinations; Table 3), species of open habitat (85%), and non-native species (95%). Excluding *C. glaucum* (70% of the total, although absent at Six-mile Creek), the greatest contributions to germination were still from non-natives (83%), forbs (67%), and species of open habitats (50%).

Based on fruit and seed morphology, 63% of the species had no special adaptation for a particular dispersal mode (Table 3, d), contributing 90% of the germinations (67% if *C. glaucum* is omitted). However, there were also 23 species with fruits specialized for dispersal by wind or ingestion by vertebrates, as well as four with ballistic, ant, or external-animal diaspore types. The majority of germinating seeds were <3 mm in length (not including long awn or pappus; Table 3, e; Electronic Supplementary

Material). The 12 species with seeds <1 mm contributed 81% of the germinations, or 36%, still the highest category, if *C. glaucum* is excluded. A few large seeds germinated (*Triticum* and *Pyrus*; 6 mm), but the occasional very large seeds found in the pellets (e.g., *Quercus* acorns; ±20 mm) had been heavily damaged by chewing or digestion.

Viable seeds were dispersed throughout the entire year, but the density and species richness of germinable seeds per pellet group varied over time (Fig. 1a, b). The highest median densities were in October, January, and February, which also had the greatest median richness (4–5 species per pellet group). Maximum numbers of seeds per pellet group reached highs in October and August, due to *C. glaucum*, but October also had 11 species in each of two pellet groups. Of the two periods when seed density and richness were relatively low (late autumn and spring), the spring low was more pronounced: at McGowan's, 14 of 19 pellet groups collected from 29 April to 21 June had no germinations, and the maximum was two seeds per pellet group. Six-mile Creek showed similar patterns, with very low density and richness in May and June, when seeds of many species are not yet mature. With the exception of *C. glaucum*, which was not present at Six-mile Creek, the two sites had similar seed abundance over the May–September period: monthly means averaged 5.3 seeds per pellet group for Six-mile Creek (Table 1), versus 5.6 for those months at McGowan's if *C. glaucum* is ignored.
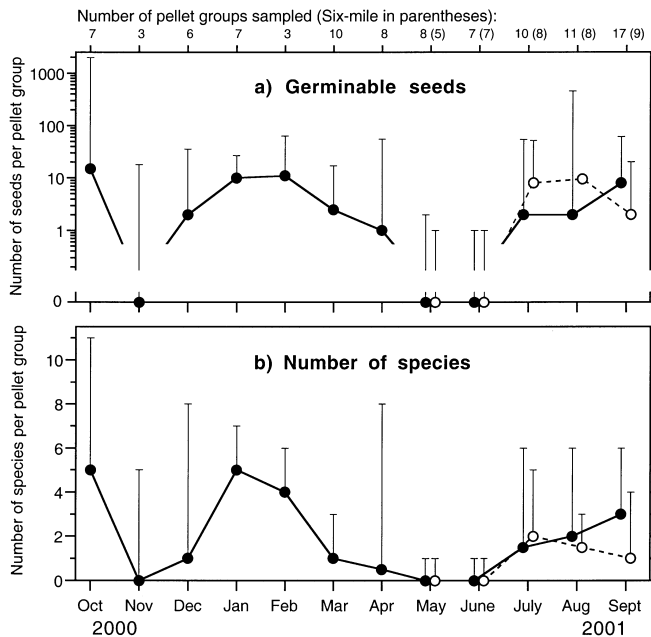

Fig. 1 Variation over the year in density and richness of germinable seeds in feces of white-tailed deer: monthly medians (*circles*) and maximum values (*bars*) for numbers of **a** seeds germinating per pellet group, and **b** species per pellet group, from the full-year samples at McGowan's Woods (*filled circles*), and the Six-mile Creek Woods samples (*open circles*; May–September). Values shown are from 1–3 collection dates per calendar month: sample sizes of pellet groups for each month are listed at the top of the figure

Table 2 Species germinating from white-tailed deer feces collected at two sites, showing totals, maximum germinations per pellet group, and frequency (of 97 pellet groups from McGowan's, 37 from Six-mile Creek). Species found in an initial set of McGowan's samples from July to August 2000 (33 pellet groups) are indicated with *asterisks*. A total of 72 identifiable taxa germinated. *Square brackets* indicate other taxa that were not counted: either because they could not be identified to species and may thus have included species already listed (*§*); or because the seeds did not germinate (values shown in parentheses), although appearing viable when cut open at the end of the study (*†*). Nomenclature follows Gleason and Cronquist (1991)

	McGowan's Woods Full year (October 2000–September 2001)			Six-mile Creek Woods Summer (May–September 2001)		
	Total	Maximum	Frequency	Total	Maximum	Frequency
Forbs						
Amaranthus hybridus	2	2	1%			
A. retroflexus	2	1	2%			
[*Amaranthus* spp.] §	15	6	4%			
Aster lanceolatus	4	2	3%			
Capsella bursa-pastoris	6	3	3%			
Chenopodium album	76	47	8%	1	1	3%
C. glaucum *	2,535	1,898	12%			
Chrysanthemum leucanthemum *						
Coronilla varia	1	1	1%	3	1	8%
Epilobium coloratum	8	5	4%			
Galium mollugo *				3	2	5%
Gnaphalium uliginosum	1	1	1%			
Linaria vulgaris *						
Lobelia inflata	1	1	1%			
Lotus corniculatus	3	2	2%	4	4	3%
Lycopersicon esculentum	2	2	1%			
Lythrum salicaria	189	70	9%			
Matricaria matricarioides *						
Medicago lupulina	10	5	4%	4	3	5%
Melilotus alba	25	13	5%			
[*Oxalis* spp.] †	0 (15)	.	(9%)	0 (2)	.	(3%)
Penstemon digitalis	3	2	2%			
Plantago major	55	16	15%	6	4	8%
Polygonum careyi	1	1	1%			
P. erectum *						
P. lapathifolium	6	4	2%			
P. persicaria	2	2	1%			
[*Polygonum* sp.] §	1	1	1%			
Portulaca grandiflora	1	1	1%			
P. oleracea	9	9	1%	9	6	8%
Potentilla norvegica *	116	51	8%	7	7	3%
P. recta	4	4	1%			
Ranunculus recurvatus	5	5	1%	1	1	3%
Solanum dulcamara *	63	31	10%	3	2	5%
S. nigrum	19	16	2%			
Solidago canadensis	2	2	1%			
S. gigantea	1	1	1%			
[*Solidago* sp.] §	1	1	1%			
Sonchus asper *	6	1	6%			
[*Sonchus* sp.] §	1	1	1%			
Spergularia media *						
Stellaria media *	28	13	6%	3	3	3%
Taraxacum officinale	2	2	1%			
Trifolium pratense *						
Trillium grandiflorum *						

Table 2 (continued)

	McGowan's Woods Full year (October 2000–September 2001)			Six-mile Creek Woods Summer (May–September 2001)		
	Total	Maximum	Frequency	Total	Maximum	Frequency
Veronica officinalis	6	5	2%	3	3	3%
V. peregrina *	1	1	1%			
V. serpyllifolia	1	1	1%			
Vicia tetrasperma *						
[unidentified dicot spp.] §	11	2	9%	3	1	8%
Graminoids						
Agrostis gigantea	1	1	1%			
A. stolonifera	15	8	4%			
Carex cristatella *						
[*Carex* spp.] § *	5	2	4%	1	1	3%
Dactylis glomerata *	2	1	2%			
Digitaria ischaemum	1	1	1%			
D. sanguinalis	1	1	1%			
Glyceria striata	1	1	1%			
Juncus tenuis *	33	5	15%			
Panicum capillare	5	3	3%			
Phleum pratense	6	2	5%			
Poa alsodes	3	3	1%			
P. annua	2	1	2%			
P. compressa *	29	6	12%	1	1	3%
P. pratensis *	8	2	7%	1	1	3%
Puccinellia distans	1	1	1%			
Sorghum bicolor (*)	4	2	2%			
Triticum aestivum *	1	1	1%			
[unidentified grass spp.] § *	1	1	1%			
[unidentified graminoid spp.] §	7	3	5%			
Woody plants						
Betula lenta				12	8	14%
[*Cornus racemosa*] †				0 (2)		(3%)
[*Crataegus* sp.] †	0 (18)		(4%)			
Juniperus virginiana	1	1	1%			
Liriodendron tulipifera *						
Lonicera aff. × *bella* *	71	31	11%	141	34	43%
Pyrus sp. (*i.e. Malus*)	1	1	1%	0 (1)		(3%)
Rhamnus cathartica	2	1	2%			
[*Rhus typhina*] †	0 (3)		(2%)			
Rosa multiflora	5	4	2%			
Rubus allegheniensis				1	1	3%
R. flagellaris				1	1	3%
R. idaeus *				2	2	3%
R. occidentalis				2	2	3%
[*Rubus* spp.] § (*)	0 (14)		(2%)	5	5	3%

The species composition of seeds in deer feces also varied over the year (see Electronic Supplementary Material). For the full-year McGowan's samples, the most abundant taxa in summer were *C. glaucum*, *Lonicera* spp., *C. album*, and *P. norvegica*. In autumn, *C. glaucum* and *P. norvegica* were still abundant, along with *Lythrum salicaria*. In winter, the largest numbers of seeds were of *L. salicaria* and *Plantago major*, while in spring only *L. salicaria* was numerous. *L. salicaria* germinated in samples from six months between October and April, while *P. major* and *J. tenuis* were dispersed in every season of the year. At least 31 species were dispersed in autumn at McGowan's (see Electronic Supplementary Material), spring had a total of 15 species in spite of low

Table 3 Characteristics of the species germinated from white-tailed deer feces, collected at McGowan's Woods and Six-mile Creek Woods between July 2000 and September 2001 (167 pellet groups total), for the 72 identifiable plant taxa (see Electronic Supplementary Material for details)

	Species	Percentage (n=72)	Contribution to germination
(a) Growth habit			
Forb	44	61	90%
Graminoid	17	24	3%
Woody	11	15	7%
(b) Habitat			
Open	58	81	85%
Wetland	5	7	7%
Forest	5	7	0.2%
Mixed	4	6	8%
(c) Origin			
Non-native to northeastern USA	46	64	95%
Native	23	32	2%
Mixed-origin species	3	4	2%
(d) Diaspore type			
No special morphology	45	63	90%
Fleshy, edible "fruit"	12	17	9%
Wind (wing or plume)	11	15	1%
Ballistic	2	3	0.2%
Hooked	1	1	0.03%
Ant	1	1	0.004%
(e) Seed length			
<1 mm	12	17	81%
1 to <2 mm	24	33	7%
2 to <3 mm	20	28	5%
3 to <7 mm	16	22	7%

numbers per pellet group, and the other two seasons were in between.

Discussion

White-tailed deer clearly disperse germinable seeds of a large number of species. At McGowan's Woods, based on our average of 38 germinations per pellet group over the year, and with a daily defecation rate of 35 pellet groups per deer (Rogers 1987) and a local density of 20 deer per km^2 (P. Curtis, Cornell University; personal communication), we estimate that a mean of 10 viable seeds per m^2 are deposited by white-tailed deer each year. Given the wide-ranging daily movements of white-tailed deer, and typical times between ingestion and deposition of up to several days (Mautz and Petrides 1971; Gonzalez-Espinosa and Quintana-Ascencio 1986), the seeds are likely to be dispersed hundreds to, occasionally, thousands of meters (Vellend et al. 2003), and even farther during seasonal migration (Halls 1984). White-tailed deer forage in a diversity of habitats, and there is no reason to suspect

that our forest samples differ in any way from pellet groups deposited throughout their home ranges (>100 ha in some regions; Lesage et al. 2000). White-tailed deer are thus significant vectors for seed dispersal across the landscape, which until now have been largely overlooked.

Viable seeds in white-tailed deer feces from our two study sites represented over 72 plant species, covering the full range of dispersal modes, habitat types, and growth forms in the local flora, and including many native and non-native species. Considering the broad array of plants in the diet of white-tailed deer, and high deer densities in many parts of their range (Halls 1984), many additional plant species are undoubtedly dispersed as well. Other species that have been reported from feces of white-tailed deer are *Conopholis americana*, a parasitic herb on oak roots (Baird and Riopel 1985), the wetland herb *Ranunculus scleratus* (Campbell and Gibson 2001), honey mesquite, *Prosopis glandulosa* (Kramp et al. 1998), and two species of *Opuntia* cactus (Gonzalez-Espinosa and Quintana-Ascencio 1986). Janzen (1985) documented white-tailed deer in Costa Rica dispersing large numbers of viable seeds of *Spondias mombin*, but not by defecation; deer regurgitated the 20-mm hard endocarps intact.

The seeds germinated from white-tailed deer feces from our study sites were predominantly alien forbs of open habitat (38% of the species), and small-seeded species (<2 mm). Differences in relative abundance among species were probably due primarily to local forage availability and feeding preferences, as deer graze on a wide variety of plants in both forested and open habitats (Halls 1984; Rouleau et al. 2002). The predominance of introduced species in our samples reflects their abundance in the many nearby open areas, including active and abandoned fields, lawns, and roadsides. Obviously not every germinable seed in the feces of white-tailed deer will establish, especially for field plants deposited in forests, or pellet groups with very high densities of seeds. The proportion of seedlings that emerge from deer feces may be similar to other natural establishment rates, given that pellet groups usually disintegrate within weeks (Wigley and Johnson 1981), although some seeds may be damaged, e.g., by insect activity in the dung. We have observed *Lonicera* seeds germinating from deer feces in situ at Six-mile Creek (Vellend 2002).

There are several potential reasons why we found only three forest herbs (*T. grandiflorum*, *Ranunculus recurvatus*, *Poa alsodes*) in our fecal samples, despite a rich herb layer (>30 species) at both forests. In contrast to field annuals that often have many thousands of seeds per plant (Salisbury 1964), most perennial forest herbs produce few seeds (often <25 per plant; Bierzychudek 1982). Also, while many forest herbs are known to be heavily browsed by white-tailed deer, forage in crop fields can be preferred (Augustine and Jordan 1998), and fields were adjacent to both our sampled forests. Another potential reason is that the relatively large seeds (e.g., 2–6 mm) of many forest herbs could be killed by chewing and digestion, as small, hard-coated seeds are less likely to be damaged by ruminants (Gardener et al. 1993), although there were

several species with large, thin-coated seeds that did germinate in our samples (e.g. *Triticum*). While many forest herbs require warm stratification to germinate (Baskin and Baskin 1998), we are confident there were no other forest herb species in the remaining ungerminated seeds sorted from pellet groups, because we compared them to published seed keys and to seeds collected from plants in our forests. Probably many more fecal samples, from larger expanses of herb-rich forest, would be necessary to document the occasional forest herb seeds dispersed by white-tailed deer. This pattern of mostly small-seeded, unspecialized diaspores, of plants of open habitat, has also been found in fecal samples from several wild mammal species in a European forest (Heinken et al. 2002). However, it is important to consider that for species such as forest herbs that produce few seeds, mainly spread only locally (by ants, ballistically, or with no other dispersers), the relative importance of any seeds carried long distances by deer can be large, even if the number of viable seeds dispersed is small.

Dispersal modes

Our results have important implications for inferring dispersal ability from diaspore type. The samples from white-tailed deer contained 45 species with small dry fruits often described as having no special dispersal morphology, also considered unassisted or gravity-dispersed (i.e., simply falling from the plant). Of the 72 total species that germinated, 40 (mostly ones lacking specialized diaspores) have also been reported in dung of other large herbivores, including cow, horse, sheep, or European deer species (Ridley 1930; Dore and Raymond 1942; Salisbury 1964; Welch 1985; Müller-Schneider 1986; Malo and Suárez 1995; Campbell and Gibson 2001; Heinken et al. 2002; Pakeman et al. 2002). Although large herbivores digest many of the seeds, and are thus seed predators, these studies have documented that they also disperse a long list of species—especially forbs and grasses having small seeds with no special diaspore morphology—via endozoochory. Regardless of whether this is "accidental" dispersal of seeds eaten along with foliage or intentional feeding on seeds and fruits (van der Pijl 1982), and whether or not these plants actually have adaptations for dispersal by large herbivores (Janzen 1984), to assume that such species lack long-distance dispersal and therefore have poor colonization ability (e.g., Singleton et al. 2001; Miller et al. 2002) is clearly erroneous. One of the adaptive traits Janzen (1984) proposed for such species was retention of seeds on the plant; it is notable that many seeds we found in white-tailed deer feces in autumn and winter were from species that would have senesced by this time, with seeds held above the snow on the old stalks. Thus, many of the species with numerous small, hard seeds that remain on the plant after ripening, and that are dispersed by large herbivores, should be considered endozoochores despite the apparent lack of specialized diaspore morphology.

Dispersal by large herbivores is not limited to species with small hard seeds, although these are typically predominant: diaspores of a variety of types can be spread by endozoochory (see also Bruun and Fritzbøger 2002; Heinken et al. 2002). We found that white-tailed deer potentially contribute a long-distance component to the seed shadows of several species with ballistic, ant, or hooked diaspore types, as well as a number of wind-dispersed species and ones with fleshy endozoochorous fruits. Many fruits may be eaten intentionally, rather than passively with foliage: Lay (1965) found remains of fleshy fruits of nearly 30 woody species in the feces of white-tailed deer. In addition to endozoochory, large herbivores are known to disperse a range of diaspore types externally on their fur or hooves, including many small-seeded species lacking specialized morphology (Ridley 1930; Heinken et al. 2002). Thus seed dispersal by large herbivores of species with other primary dispersal modes potentially complicates any predictions of dispersal ability and seed shadows based simply on diaspore type. Seed dispersal of such species will need to be modeled as a stratified process, incorporating local and long-distance movement by the multiple vectors into an overall seed shadow (Cain et al. 2000). The long-distance component is generally more difficult to quantify, but for species whose seeds are dispersed by white-tailed deer, the quantitative form of the deer-generated component has been estimated (Vellend et al. 2003), allowing more realistic models of dispersal and migration to be constructed.

Implications for plant migration and invasive spread

In many cases, white-tailed deer may be the most important vector for long-distance seed dispersal, with consequent implications for plants colonizing new habitats across landscapes as well as for post-glacial migration. Because of the vastly disproportionate effect of long-distance dispersal events, even if rare, on migration rates (Cain et al. 1998), deer may make a significant contribution even for species whose seeds are dispersed very infrequently. A recent conceptual paper (Pakeman 2001) and a review (Gill and Beardall 2001) have highlighted the potential importance of deer species for long-distance dispersal of plants. Just as with white-tailed deer in eastern North America, empirical studies in Europe and Asia have documented that other species of deer also disperse viable seeds of a number of species (Welch 1985; Dinerstein 1989; Malo et al. 2000; Heinken et al. 2002).

Among the plants native to eastern North America in our samples, white-tailed deer may have helped facilitate the post-glacial migration of over a dozen native herbs and grasses of open or wetland habitats, most of which have no special diaspore morphology, as well as several wind-dispersed trees, bird-dispersed woody plants, and forest herb species. Because our samples did not contain seeds of the many other forest herbs in the two stands, it remains unclear to what extent white-tailed deer might help explain the post-glacial migration, or the colonization of post-

agricultural stands, by forest herbs in North America. However, the presence of native *Solidago* and *Aster* species in our samples suggests that perhaps their expansion into the old fields they now dominate, from their original isolated patches of natural unforested habitat (Marks 1983), might have been facilitated by white-tailed deer as well as wind dispersal.

There are also a number of practical implications of long-distance seed dispersal by deer for the spread of introduced species. Our samples contained germinable seeds of four of the 20 invasive species of greatest concern in New York State (Winters and Quillen 2001). Three are shrubs known also to be dispersed by birds (*Lonicera* spp., *Rosa multiflora*, and *Rhamnus cathartica*), but for the fourth, purple loosestrife (*Lythrum salicaria*), deer could be a very important vector for invasive spread to wetlands across North America. Purple loosestrife seeds have no specialized morphology and are thought to be dispersed primarily by water (Mal et al. 1992): white-tailed deer provide a means of upstream spread and overland dispersal to new watersheds. Invasive plant spread may be greatly enhanced if white-tailed deer are preferentially feeding on these species: further studies are needed to address this question.

Another practical implication of our findings is that 27 of the species we found are considered weeds in northeastern USA (of crops, pastures, or lawns; Uva et al. 1997), and 11 species, including *C. glaucum*, are classified as noxious weeds in Québec, Canada (www.canlii.org/qc/regu/crqc/20030911/r.q.a-2r.1/whole.html). Although domestic animals, manuring of fields, and farm machinery disperse many agricultural weeds (Ridley 1930; Poschlod and Bonn 1998; Bruun and Fritzbøger 2002), deer could carry the species to more remote habitats. The presence of viable crop seeds in the deer feces (e.g., tomato and wheat; *Lycopersicon*, *Triticum*) indicates a potential mode of spread for genetically-modified plants. It is possible deer have helped facilitate the escape of some plants from cultivation: 14 of the species we found are both cultivated and escaped in northeast USA (Gleason and Cronquist 1991; Uva et al. 1997), including the garden flower *Portulaca grandiflora* (with small seeds that simply fall from the capsule), which has only recently become naturalized in the local flora (F.R. Wesley, Cornell; unpublished data). Finally, another potential implication is that dispersal by deer may also contribute to the soil seed bank of field species in forests (as the former practice of allowing cattle to graze in forests is likely to have done), as well as to the colonization of woody and herbaceous plants into old fields.

Conclusion

In this paper, we have reported the discovery of a formerly unappreciated, but probably quite important, vector for seed dispersal in eastern North America: white-tailed deer. In spite of the many negative consequences of browsing on plants, white-tailed deer may also provide a positive influence by facilitating seed dispersal, with consequent potential effects on population and community structure, and the ability of species distributions to track climate or land-use changes. It is likely that white-tailed deer contribute an important long-distance component to the seed shadows of hundreds of plant species.

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