

Exotic Seed Dispersal by White-tailed Deer in Southern Connecticut

Author(s): Scott C. Williams and Jeffrey S. Ward Source: Natural Areas Journal, 26(4):383-390. Published By: Natural Areas Association

DOI: http://dx.doi.org/10.3375/0885-8608(2006)26[383:ESDBWD]2.0.CO;2

URL: http://www.bioone.org/doi/full/10.3375/0885-8608%282006%2926%5B383%3AESDBWD

%5D2.0.CO%3B2

BioOne (<u>www.bioone.org</u>) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

RESEARCH ARTICLE

Exotic Seed Dispersal by White-tailed Deer in Southern Connecticut

Scott C. Williams¹ Jeffrey S. Ward

Department of Forestry and Horticulture
The Connecticut Agricultural Experiment
Station
123 Huntington Street
Box 1106

•

New Haven, CT 06504

¹ Corresponding author: scott.williams@po.state.ct.us; 203-974-8527

Natural Areas Journal 26:383–390

ABSTRACT: We examined the role of suburban white-tailed deer (*Odocoileus virginianus* Zimmerman) in dispersal of exotic plants in forests bordered by medium-density housing in southern Connecticut. Estimated deer density on the research site was 23 deer/km² with higher local densities along the suburban/woodland interface. In 2002, 90 pellet groups were gathered periodically from September through December. In 2003, eight pellet groups were collected weekly from early June through late December for a total of 236. All pellet groups were vernalized at 5°C for 60 days. Pellet groups were placed in a growing medium in trays in a temperature controlled greenhouse for six months. Seeds germinated from 47% of pellet groups, which included 656 seedlings of 57 species. Seeds (n = 326) of 32 species not native to Connecticut germinated in 23% of pellet groups. We estimated that the deer herd on site had the potential to disperse 586-1046 viable exotic seeds/day/km² during the 2002 sampling period and 390-696 viable exotic seeds/day/km² during the 2003 sampling period. Birds, small mammals, and abiotic factors are known dispersal agents for exotic plants, some of which are invasive. Our results indicate that white-tailed deer are another important dispersal agent of exotic species. Thus, white-tailed deer may not only alter vegetation structure through direct browse damage of established plants, but also indirectly by lowering reproductive output of native plants and simultaneously distributing seeds of exotic species.

Index terms: exotic, foliage, fruit, pellet groups, seed dispersal, white-tailed deer

INTRODUCTION

Exotic plant invasions are the cause for significant ecological and economic damage (Blaustein 2001, Costello and McAusland 2003). The United States has approximately 5000 established exotic plant species, some of which are invasive and competing with 17,000 native species (Pimentel et al. 2000). Exotic species are spreading and invading wildlife habitat, displacing numerous native species in the process (Morse et al. 1995).

The invasion of woodlands by exotic plants is particularly noticeable in areas adjacent to suburban neighborhoods. Such areas are becoming more common throughout the United States as demand for development increases habitat fragmentation. This suburban/woodland interface has created ideal habitat for white-tailed deer (Odocoileus virginianus Zimmerman) with an abundance of food and protection from hunting and predation (DeNicola et al. 2000). Such areas often experience severe browsing rates of both native and ornamental plant species. Many residents establish gardens with a high proportion of ornamental exotics. These gardens provide a potential seed source for dispersal into adjacent wooded areas.

Until recently in the United States, the potential role of white-tailed deer in the dispersal of native, cultivated, and/or exotic seeds has been largely ignored. Vellend

(2002) documented deer as vectors for dispersing honeysuckle (*Lonicera* L.). Vellend et al. (2003) documented deer as dispersing agents for a native species – *Trillium grandiflorum* ((Michx.) Salisb.). Myers et al. (2004) described deer as a long distance dispersal mechanism for numerous species of plants, including exotics. Our study investigated the role of freeranging white-tailed deer on dispersal of exotic seeds along the suburban/woodland interface in Connecticut.

On our study site, female white-tailed deer (does) had a mean annual home range of approximately 80 ha (Ramakrishnan and Williams, unpubl. data). Deer often browse ornamental and landscape plantings within suburban areas during twilight hours. They retreat to adjacent forested areas during daylight, inevitably defecating and depositing seeds on the forest floor. Does who utilize the suburban/woodland interface within their range can transport seeds anywhere, from several hundred meters to over 3 km (Vickery et al. 1986, Vellend et al. 2003).

Because does have overlapping home ranges, exotic species that germinate and mature in adjacent forests may spread throughout the forest interior. In several growing seasons, does could potentially transport viable seeds many kilometers from suburban areas into wooded ones. Adult male deer (bucks) on the study site comprised approximately 20% of the

population based on vehicular transect data (Ramakrishnan and Williams, unpubl. data), but ranged over larger areas than does. They may transport seeds up to 10 km or further.

Deer probably ingest most seeds unintentionally as they browse. Seeds that would be able to withstand passage through a ruminant digestive tract would most likely be small and have a tough outer coating (Janzen 1984). It is unlikely that seeds of plants with fleshy, succulent fruits would be found in deer feces in any great abundance, as these types of seeds are usually fed upon and transported by birds (Willson 1986). The morphology of plants described by Janzen's (1984) "foliage is the fruit" hypothesis work on nearly the same principle. Plants of this nature have small and inconspicuous seeds proximate to palatable foliage. The hypothesis states that these small-seeded plants use incidental ingestion by large herbivores as a primary mode of dispersal. Seeds of this type were previously thought to be dispersed simply by gravity or surface water runoff (Janzen 1984), but unexplained long-distance dispersals of certain plant species have led researchers to look elsewhere (Myers et al. 2004). We expected the majority of exotic species that germinated from gathered pellet groups to exhibit this type of morphology.

White-tailed deer may play a role in the expansion of exotic species via three mechanisms: (1) increasing available growing space for new seedlings, (2) lowering reproduction output of native species, and (3) dispersal of exotic seeds. Waller and Alverson (1997) stated that in suburban areas, adverse effects of deer browsing are compounded by the invasion of woody and herbaceous exotic plant species. Casual observations suggest that deer dispersing seeds of cultivated and/or exotic species from suburban neighborhoods into adjacent woodlands further compound this problem. To examine this possibility, we gathered and planted deer pellet groups to determine which types of seeds would remain viable after passing through a ruminant digestive tract and could successfully germinate from intact pellets.

MFTHODS

Study Site and Deer Population

This study was conducted on the South Central Connecticut Regional Water Authority's Lake Gaillard property in southern Connecticut (41°21'N, 72°46'W) in the town of North Branford. The property is privately owned, closed to the public, and covers an area of approximately 2800 ha including a 400 ha reservoir. The property is managed for water quality with some commercial timber harvesting. Our research area was restricted to the 1550 ha bounding the reservoir to the south and extending northward. The property, excluding the reservoir, is approximately 90% forested with some fields and a spruce (Picea spp.) plantation at the south end.

The property north of the reservoir extends several kilometers and is considerably further from residential settlements. Legal hunting has been prohibited since the mid-1920s, which has fostered a large deer population. Based on four different censusing techniques (mark/recapture survey, walking line transect method, vehicle line transect method, aerial snow count), deer density was calculated at approximately 23 deer/km² throughout the study area in 2003. Portions of the southern population were estimated at 40 deer/km² while portions of the northern population were estimated at 14 deer/km² (Ramakrishnan and Williams, unpubl. data). Similar densities were reported in 1991 using pellet counts (Ward and Stephens 1995). Southern does had been observed utilizing residents' backyards and gardens as part of their range, while northern does seldom wandered into adjacent suburban areas.

Dominant tree species on site are oak (*Quercus* spp.), sugar maple (*Acer saccharum* Marsh.), tulip poplar (*Liriodendron tulipifera* L.), black birch (*Betula lenta* L.), and American beech (*Fagus grandifolia* Ehrh.). Because of high deer densities, very little woody understory vegetation is present except for sugar maple seedlings less than 10 cm tall, Japanese barberry (*Berberis thunbergii* DC.), winged burning bush (*Euonymus alata* (Thunb.) Sieb.),

wine raspberry (*Rubus phoenicolasius* Maxim.), and cat greenbriar (*Smilax glauca* Walt.). Autumn olive (*Elaeagnus umbellate* Thunb.) has become well established in abandoned fields and disturbed areas. Medium-high density residential communities (~ 103 residences/km²) bound the southern margin of the property.

Field procedures

Ninety pellet groups were collected from 13 September to 16 December 2002 throughout the site. An additional 236 pellet groups were collected from 2 June through 22 December 2003. In 2003, eight pellet groups were collected weekly – four each throughout the northern and southern portions of the site. We hoped to detect the time of year deer had the greatest potential to disperse exotic seeds. Coordinates of sampling locations were determined using standard 7.5-minute topographic quadrangles. Only pellet groups with a sufficient glisten were collected to insure they had been deposited since the previous sampling period. Care was taken to gather only pellets; leaf litter and soil were brushed away to prevent contamination. The entire pellet group was collected, placed in an individual sampling bag, and then vernalized at 5°C for 60 days.

After 60 days, entire pellet groups were removed and placed in pellet form on and lightly covered with the growing medium Promix® (Rivière-du-Loup, Québec, Canada). Pellet groups were individually marked and planted four to a tray. Planted pellet groups were kept in a temperature-controlled greenhouse at 24 °C. Pellet groups were watered as needed and remained in the greenhouse for approximately six months. Seedlings were allowed to grow until they could be identified, at which time they were removed from the tray and discarded. One control tray was established for every four treatment trays (16 pellet groups) in 2002 and for every eight treatment trays (32 pellet groups) in 2003. These trays were filled with only Promix®. Control trays were placed among, and watered concurrently with, trays containing pellet groups.

We determined United States native versus exotic status and seedling nomenclature using the USDA Natural Resources Conservation Service's Plants Database (USDA, NRCS 2004). Plants native to Connecticut were determined using Dowhan (1979). Species found germinating in white-tailed deer pellets were classified into five categories: (1) F – small fruits that were directly targeted by deer, (2) S – small seeds in close proximity to succulent foliage, (3) G – grasses, (4) P – prostrate plants with seeds close to foliage, and (5) R – prostate plants with raised seeds heads.

Successful establishment of new colonies, essential for maintenance of a local population, is related to both the number of seeds within a pellet group (abundance) and the number of pellet groups with at least some viable seeds. The first factor increases the likelihood of at least one plant becoming established, and the second factor increases the chances of seeds being deposited in a microsite favorable for plant germination and development.

We calculated a dispersal index that incorporated both abundance and frequency. Species were ranked from highest to lowest by both abundance and frequency of occurrence. The dispersal index for each species was then determined by ranking the mean of these two rankings. Note that lowest index value, 1, was assigned to the highest ranked species.

Nine does were fitted with global positioning system (GPS) collars on site (Lotek Wireless Inc., Newmarket, Ontario, Canada) for a separate study during our sampling interval (Ramakrishnan and Williams, unpubl. data). Collars were programmed to record locations at two-hour intervals. Average movement of animals within a 24-hour period was calculated by averaging daily ranges of five random days within each month for each collared animal during the time the collars were deployed. The minimum convex polygon method within the Animal Movement extension (Hooge and Eichenlaub 1997) of the geographic information system program ArcView (Version 3.3, ESRI, Inc. Redlands, CA) was used to determine average daily area utilized (hectares).

RESUITS

Six hundred and fifty-six seeds germinated in 47% of pellet groups. Species not native to Connecticut accounted for 326 (50%) of seedlings. We were able to positively identify 57 taxa to the species level, and five to the genus, which included graminoids, forbs, and woody species. Two species, Canadian horseweed (*Conyza canadensis* (L.) Cronq.) and yellow wood sorrel (*Oxalis stricta* L.), were found in both control and treatment trays. These species were excluded from analysis because it could not be determined if individual seedlings originated in a pellet or were the result of contamination.

Of the 57 species that germinated from pellet groups, 35 (61%) were native to the United States, 10 of which were exotic to the state of Connecticut (Table 1). Thus, only 25 species (44%) were native to Connecticut, while 32 species (56%) were exotic. The most common exotic species was Carolina horsenettle (Solanum carolinense L.) comprising 33% of exotic seedlings, followed by little hogweed (Portulaca oleracea L.) (24%), lambsquarters (Chenopodium album L.) (12%), green carpetweed (Mollugo verticillata L.) (4%), redroot amaranth (Amaranthus retroflexus L.) (4%), and star chickweed (Stellaria pubera Michx.) (3%).

Frequency (percent of seedlings with at least one seedling of a given species) was also examined. Seedlings of exotic species germinated in 23% of pellet groups. Highest frequencies were observed for Carolina horsenettle and little hogweed - coincidentally, the species with the highest number of seedlings. Seedlings of these species appeared in 8.4% and 3.3% of pellet groups, respectively. Although lambsquarters was the third most abundant species, it was only found in 0.9% of pellet groups. The less abundant hairy crabgrass (Digitaria sanguinalis (L.) Scop.), in contrast, was found in 2.1% of pellet groups. Sixteen of the species not native to Connecticut were found in only one pellet group, and in most cases, only one individual represented these species.

Using our ranking scheme, the top 10

species included Carolina horsenettle, little hogweed, redroot amaranth, hairy crabgrass, lambsquarters, autumn olive, common gypsyweed (*Veronica officinalis* L.), honeysuckle, black nightshade (*Solanum nigrum* L.), and birdfoot deervetch (*Lotus corniculatus* L.) (Table 1).

Viable exotic seeds germinated in pellet groups gathered throughout the duration of our sampling period. Greater species richness was observed for pellet groups collected in early autumn. Sixteen unique exotic species germinated in pellet groups gathered in September and 14 unique species in October. Total monthly count of germinated stems did not produce any statistically meaningful results because species such as little hogweed and Carolina horsenettle produced disproportionate numbers of seedlings relative to other species, thereby skewing monthly totals.

Forbs accounted for 64% of all germinated exotic seedlings, graminoids 18%, and woody plants accounted for an additional 18%. Species with small fruits that were directly targeted by deer (F) were found in 13% of pellet groups and accounted for 41% of exotic seedlings observed in this study.

Three of the categories fit into Janzen's (1984) "foliage is the fruit" hypothesis that the seeds are incidentally ingested by an herbivore targeting foliage. Species with small seeds in close proximity to succulent foliage (S) were found in 4% of pellet groups and accounted for 17% of seedlings. Grasses (G) were also found in 4% of pellet groups and accounted for 4% of seedlings. Prostrate plants with seeds close to foliage (P) were found in 5% of pellet groups and accounted for 32% of seedlings. The seed heads of prostrate plants with raised seed (R) may have been directly targeted by browsing deer, or consumed accidentally by deer targeting foliage - in which case this group would also fit the "foliage is fruit" hypothesis. Seedlings of this group were found in 5% of trays and accounted for 6% of seedlings.

We found a greater exotic species diversity (n = 24) in pellet groups collected a mean distance of 500 m from medium-high

Table 1. Scientific name, common name, life form (Form), life history (Life), frequency of occurrence (Freq), count of seedlings (Count), and dispersal ranking (Rank) for Connecticut exotic species that germinated directly from intact pellet groups (n = 326).

Fruit	Scientific Name	Common Name	Form	Life	Freq	Count	Rank
F	Solanum carolinense L.	Carolina horsenettle	F	P	28	106	1
	Elaeagnus umbellata Thunb.	Autumn olive	W	P	5	5	6
	Lonicera L.	Honeysuckle	W	P	4	4	8
	Solanum nigrum L.	Black nightshade	F	AP	2	7	9
	Rubus phoenicolasius Maxim.	Wine raspberry	W	P	2	6	12
	Malus sp.	Apple	W	P	2	2	17
	Rosa multiflora Thunb. ex Murr.	Multiflora rose	W	P	2	2	17
	Silene latifolia Poir. ssp. alba .	Bladder campion	F	BP	1	1	32
S	Amaranthus retroflexus L.	Redroot amaranth	F	A	5	13	4
	Chenopodium album L.	Lambsquarters	F	A	3	38	5
	Nepeta cataria L.	Catnip	F	P	2	2	17
	Polygonum persicaria L.	Spotted ladysthumb	F	AP	1	1	32
	Capsella bursa-pastoris (L.)	Shepherd's purse	F	A	1	1	32
P	Portulaca oleracea L.	Little hogweed	F	A	11	78	2
	Mollugo verticillata L.	Green carpetweed	F	A	1	14	17
	Stellaria pubera Michx.	Star chickweed	F	P	1	10	18
	Cerastium fontanum Baumg.	Mouse-ear chickweed	F	BP	1	1	32
R	Veronica officinalis L.	Common gypsyweed	F	P	4	6	7
	Veronica persica Poir.	Birdeye speedwell	F	A	3	3	11
	Lotus corniculatus L.	Birdfoot deervetch	F	P	3	3	11
	Plantago major L.	Common plantain	F	P	2	2	17
	Vicia sp.	Vetch	F	AP	1	3	19
	Sonchus asper (L.) Hill	Spiny sowthistle	F	A	1	2	20
	Barbarea vulgaris Ait. f.	Garden yellowrocket	F	В	1	1	32
	Plantago lanceolata L.	Narrowleaf plantain	F	AP	1	1	32
	Trifolium repens L.	White clover	F	P	1	1	32
G	Digitaria sanguinalis (L.) Scop.	Hairy crabgrass	G	A	7	8	4
	Agrostis capillaris L.	Colonial bentgrass	G	P	1	1	32
	Elymus repens (L.) Gould	Quackgrass	G	P	1	1	32
	Pennisetum glaucum (L.) R. Br.	Pearl millet	G	AP	1	1	32
	Sorghum halepense (L.) Pers.	Johnsongrass	G	P	1	1	32
	Zea mays L.	Corn	G	A	1	1	32

Form: W-Woody, F-Forb, G-Grass **Life:** A-Annual, B-Biennial, P-Perennial

Fruit: F – small fruits that were directly targeted by deer, S – small seeds in close proximity to succulent foliage,

P – prostrate plants with seeds close to foliage, R – prostate plants with raised seeds heads, and G – grasses

density human settlements at the south end of the study site (≈ 103 residences/km²). Fewer exotic species (n = 17) germinated in pellet groups collected a mean distance of 1600 m from medium density housing (≈ 62 residences/km²) and interspersed agricultural lands in the northern portion of the site. However, this difference was not significant using Fisher's exact test with Yate's correction for continuity (p = 0.12).

One-way ANOVA analysis of GPS collar data indicated that 24-hour range of does was not equal throughout the sampling period (p = 0.02, df = 209). Mean range size started at a low of 7.0 ha in June and increased to a high of 19.3 ha in December (Figure 1). Concurrently, there was an increase in exotic species diversity through October, followed by a decrease in November and December in 2003 (Figure 1).

Using our estimate of 23 deer/km² on site, a defecation rate of 19.6/day (Rollins et al. 1984), our sampling period of 94 days for 2002, and seedling data from

our pellet groups, we estimated that deer could potentially deposit 586 viable exotic seeds/day/km² from September through December 2002. If a defecation rate of 35/day (Rogers 1987) is used, the number increases to 1046 viable exotic seeds/day/km² for the same period. The 2003 estimate was 390 viable exotic seeds/day/km² from June through December using Rollins et al. (1984) and 696 viable exotic seeds/day/km² throughout the same period using Rogers (1987).

DISCUSSION

It appears that white-tailed deer are responsible for at least some of the dispersal of exotic species in forests bordering residential neighborhoods. Increased development and fragmentation of forests and natural areas make these areas highly susceptible to exotic invasions by providing deer with refugia free of predation and year-round access to food from nearby ornamental gardens.

Because long-distance dispersal of small-

seeded species may be rare and difficult to document (Cain et al. 2000, Myers et al. 2004), the transport of seeds by white-tailed deer is a potential mechanism for longdistance dispersal (Vellend 2002, Vellend et al. 2003, Myers et al. 2004). As at least one exotic seedling was found in 24% of pellet groups, the deer at our study site have the potential to establish new colonies of exotic plants some distance from established plants during June through December. In addition, browsing deer can lower reproductive output of native species by reducing plant size or direct browsing of flowers (Fletcher et al. 2001, Webster et al. 2001, Frankland and Nelson 2003). While some populations may recover following release from browse pressure (Anderson et al. 2002, Townsend and Meyer 2002), re-establishment of viable populations following local extirpation may be delayed because many species have short dispersal distances (Carson et al. 2005). The data show that deer are capable of dispersing exotic seeds long distances that can then germinate in an over-browsed native understory. Continual long-distance dispersal by

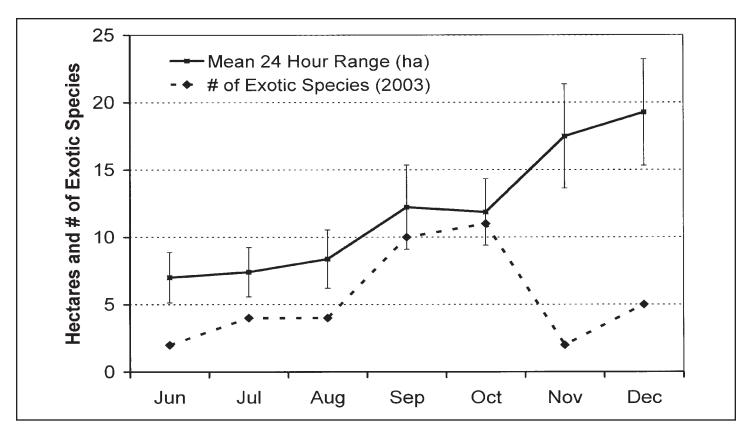


Figure 1. Mean monthly 24-hour area coverage (ha) of 9 does and number of germinated exotic species from pellet piles (n = 236) gathered each month for 2003. Brackets indicate standard error of the mean.

deer will benefit some exotic species over time – precipitating their rapid colonization to the detriment of native forest flora.

The relationship between total abundance and frequency of occurrence is an important one for successful establishment of exotic species in the landscape. Total seedling abundance is only one component of effective seed dispersal. Multiple seedlings of the same species germinating from one pellet group on a favorable microsite would compete with one another resulting in only a few, if any, survivors. However, high seedling abundance in conjunction with dispersal at multiple locations (high frequency) would increase the chances of successful germination and development. Species that had multiple seedlings in multiple pellet groups (e.g., Carolina horsenettle, little hogweed, and redroot amaranth), would most likely disperse long distances over time and successfully establish on the forest floor because of consumption and transport by deer.

Many of the exotic species we observed germinating in pellet groups could employ Janzen's (1984) "foliage is the fruit" for seed ingestion to provide a mechanism for medium to long-distance dispersal. Plants utilizing this mechanism of dispersal produce a high number of small seeds and are often highly nutritious deer forage. For instance, little hogweed, more commonly known as purslane, has its seeds enclosed in a small, round capsule (Niering et al. 1995). Little hogweed is nutritious with high levels, relative to other vegetables, of Omega-3 fatty acids and protein (Ezekwe et al. 1999). The seeds of redroot amaranth contain 18% protein (National Academy of Sciences 1971) and have been reported as a high quality forage for white-tailed deer in North Dakota (Dittberner and Olson 1983). Lambsquarters is a common weed capable of producing thousands of small seeds proximate to edible foliage and is high in beta-carotene and vitamin C (Lu et al. 2001). The foliage as the attractant strategy insures more seeds will germinate away from the parent plant than from dispersal by wind, water, gravity, or biotic factors (Willson 1993, Myers et al. 2004). This could account, in part, for the observed widespread distribution of exotic species across the landscape.

Our results concur with Myers et al. (2004) that the fruit of some herbaceous species may be directly targeted. Carolina horsenettle produces tomato-like fruits and had the highest dispersal ranking. Its relatively high abundance and frequency in our pellet groups strongly suggest these fruits were targeted for consumption by deer. In addition, these fruits are large enough (10-15 mm) that incidental ingestion is not likely. Although numerous seedlings of exotic species with fleshy fruits were observed (Table 1), transport by birds is probably a more important mechanism for their dispersal (Willson 1986, Loiselle 1990, Herrara et al. 1994, Orrock 2005). Transport by deer may provide a mechanism for dispersal within a habitat (e.g., open field, closed canopy forest). Lay (1965) documented the presence of multiple species of fleshy fruits in white-tailed deer feces in the southern United States. Willson (1993) suggests deer are capable of transporting small seeds, such as those found in fleshy fruits, without damaging them by way of digestion. Autumn olive was the only other fruiting species in the top 10, as it had five seedlings in five different pellet groups. Deer have been known to browse autumn olive foliage (I.M. Ortega, foraging ecologist, University of Connecticut, pers. comm.) and may either accidentally ingest or directly target the fruits.

During periods of low browse availability in the 2003 sampling period, deer were witnessed actively seeking out and consuming fruits of Japanese barberry adjacent to sampling areas. Ehrenfeld (1997) suggests that white-tailed deer disperse this species. It is uncertain whether the lack of barberry seedlings in our pellet groups was due to low sampling frequency (relative to total defecation rates), or whether barberry seeds are easily digested, or are incapable of breaking through the pellet encapsulation. Japanese barberry seeds were not documented in deer feces by Myers et al. (2004).

Our dispersal estimates of 586-1046 germinable exotic seeds/day/km² for 2002 and 390-696 germinable exotic seeds/day/km² for 2003 are approximations for the study

area and sampling period based on germination results and varying defecation rates. Undoubtedly, these estimates will vary regionally and annually depending on local deer densities, exotic species densities and seed production, and other factors. However, it is evident that deer play a significant role in dispersal of exotic seeds. The greatest diversity of exotic species germinated in pellet groups gathered in September and October, corresponding to the period of maximum seed production.

Ranges of does during 24-hour intervals increased throughout our sampling period (Figure 1). We suspect smaller ranges existed in summer months while does were tending fawns (Ozoga et al. 1982, Scanlon and Vaughan 1985). Ranges of does tend to increase as fawns are weaned, become more self-sufficient, and less susceptible to predation. As ranges increase, deer are more likely to encounter and consume seeds from a greater variety of plant species, including exotics. Ranges may have increased and number of exotics may have decreased in November due to the breeding season. Both bucks and does were probably preoccupied with breeding or trying to avoid it, and reduced their food (and exotic seed) intake as a result. Exotic species diversity then increases in December, after the breeding season, when animals turn their attention back to feeding in preparation for winter.

It is interesting to note that seed maturity of many exotic species is synchronized with this period of increased home range size. Many plant species exotic to the United States co-exist with cervids in their country of native origin. For instance, China is the country of origin for American exotic such as multiflora rose (Rosa multiflora Thunb. ex Murr) and wine raspberry and also to cervids such as tufted deer (Elaphodus cephalophus Milne-Edwards), Chinese water deer (Hydropotes inermis Heude), and white-lipped deer (Cervus albirostris Przewalski). Japan is also home to many American exotics (wine raspberry, Japanese barberry, multiflora rose) and home to the native sika deer (Cervus nippon Temminck). Reproduction, gestation, and parturition of these deer are similar to our native white-tailed deer: the rut in October

and November followed by the birth of fawns in May/June (Geist 1998). Thus, the synchronization of seed maturation during the period of home range expansion may be a co-evolved strategy for long-distance seed dispersal that has proven successful in a new locale with a new, but similar, cervid species.

Although Vellend (2002) and Myers et al. (2004) demonstrated that white-tailed deer can transport viable seeds of exotic species, the contribution of white-tailed deer to the encroachment and expansion of exotics species into protected natural areas is probably greater than has been previously documented. Earlier studies that illustrated the role of severe browsing in limiting growth and reproduction of native species, or the destruction of plants by repeating browsing, may not have fully elucidated the influence of large deer herds in modifying community structure. White-tailed deer are one mechanism for transportation of exotic species into, and establishment in, depauperated habitats created by overbrowsing. Limiting the size and growth of white-tailed deer populations near the suburban/woodland interface would help to prevent, or at least reduce, the further spread of undesirable exotic plant species and help to maintain viable native plant populations.

ACKNOWLEDGMENTS

We would like to thank the South Central Connecticut Regional Water Authority for allowing access to their property, J. P. Barsky for assistance with pellet collection, plant identification, and photography, and E. Belinsky and J. Berlanda for assistance with watering and greenhouse maintenance. We would also like to thank F. J. Ferrandino for assistance with data analysis and I. M. Ortega for comments on this manuscript.

Scott Williams is a Wildlife Research Technician studying the impacts overabundant white-tailed deer have on natural and managed ecosystems. He is a Ph.D. candidate in wildlife management at the University of Connecticut.

Jeff Ward is the Chief Scientist of the Department of Forestry and Horticulture. His research has focused on long-term population dynamics of woody plants in natural areas, growth response of individual trees following stand disturbance, and methods of reducing deer browse damage in forest plantations.

LITERATURE CITED

- Anderson, C.E., K.A. Chapman, M.A. White, and M.W. Cornett. 2002. Effects of browsing control on establishment and recruitment of eastern white pine (*Pinus strobus* L.) at Cathedral Grove, Lake Superior Highlands, Minnesota, USA. Natural Areas Journal 22:202-210.
- Blaustein, R.J. 2001. Kudzu's invasion into southern United States life and culture. Pp. 55-62 *in* J.A. McNeeley, ed., The Great Reshuffling: Human Dimensions of Invasive Species. The World Conservation Union, IUCN, Gland, Switzerland and Cambridge, U.K.
- Cain, M.L., B.G. Milligan, and A.E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87:1217-1227.
- Carson, W.P., J.A. Banta, A.A. Royo, and C. Kirschbaum. 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. Natural Areas Journal 25:10-18.
- Costello, C., and C. McAusland. 2003. Protectionism, trade, and measures of damage from exotic species introductions. American Journal of Agricultural Economics 85:964.
- DeNicola, A.J., K.C. VerCauteren, P.D. Curtis, and S.E. Hygnstrom. 2000. Managing white-tailed deer in suburban environmentsa technical guide. Cornell Cooperative Extension, the Wildlife Society Wildlife Damage Management Working Group, and the Northeast Wildlife Damage Research and Outreach Cooperative, Ithaca, N.Y.
- Dittberner, P.L., and M.R. Olson. 1983. The plant information network (PIN) data base: Colorado, Montana, North Dakota, Utah, and Wyoming. FWS/OBS-83/86, U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- Dowhan, J.J. 1979. Preliminary checklist of the vascular flora of Connecticut (growing without cultivation). Report of Investigations No. 8, State Geological and Natural History Survey of Connecticut, The Natural Resources Center, Department of Environ-

- mental Protection. Hartford.
- Ehrenfeld, J.G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC.). Journal of the Torrey Botanical Society 124:210-215.
- Ezekwe, M.O., A.T.R. Omara, and M. Tadesse. 1999. Nutritive characterization of little hogweed accessions as influenced by planting date. Plant Foods for Human Nutrition (Dordrecht) 54:183-191.
- Fletcher, J.D., W.J. McShea, L.A. Shipley, and D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. Natural Areas Journal 21:172-176.
- Frankland, F., and T. Nelson. 2003. Impacts of white-tailed deer on spring wildflowers in Illinois, USA. Natural Areas Journal 23:341-348.
- Geist, V. 1998. Deer of the World. Stackpole Books, Mechanicsburg, Pa.
- Herrera, C.M., P. Jordano, L. Lopez-Soria, and J.A. Amat. 1994. Recruitment of a mastfruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs 64:315-344.
- Hooge, P.N., and B. Eichenlaub. 1997. Animal movement extension to arcview, ver.
 1.1. Alaska Science Center Biological Science Office, U.S. Geological Survey, Anchorage.
- Janzen, D.H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. The American Naturalist 123:338-353.
- Lay, D.W. 1965. Fruit utilization by deer in southern forests. Journal of Wildlife Management 29:370-375.
- Loiselle, B.A. 1990. Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. Oecologia 82:494-500.
- Lu, Z., R.M. Hodges, C.J. Mota-Urbina, P.L. Gallawa, R. Chaturvedi, and C.N. Hodges. 2001. Nutrient constituents of salicornia (*Salicornia bigelovii* Torr.) a seawater-irrigated new green vegetable. Hortscience 36:484.
- Morse, L.E., J.T. Kartesz, and L.S. Kutner. 1995. Native vascular plants. Pp. 205-209 *in* E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, eds., Our living resources: a report to the nation on the distribution, abundance, and health of US plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.
- Myers, J.A., M. Vellend, S. Gardescu, and P.L. Marks. 2004. Seed dispersal by white-

- tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. Oecologia 139:35-44.
- National Academy of Sciences. 1971. Atlas of nutritional data on United States and Canadian feeds. National Academy of Sciences, Washington, D.C.
- Niering, W.A., N.C. Olmstead, S. Rayfield, and C. Nehring. 1995. National Audubon Society Field Guide to North American Wildflowers, 15th ed. Alfred A. Knopf. New York.
- Orrock, J.L. 2005. The effect of gut passage by two species of avian frugivore on seeds of pokeweed, *Phytolacca americana*. Canadian Journal of Botany 83:427-431.
- Ozoga, J.J., L.J. Verme, and C.S. Bienz. 1982. Parturition behavior and territoriality in white-tailed deer: impacts on neonatal mortality. Journal of Wildlife Management 46:1-11.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53-65.
- Rogers, L.L. 1987. Seasonal changes in defection rates of free-ranging white-tailed deer. Journal of Wildlife Management 51:330-333.

- Rollins, D., F.C. Bryant, and R. Montandon. 1984. Fecal ph and defecation rates of eight ruminants fed known diets. Journal of Wildlife Management 48:807-813.
- Scanlon, J. J., and M.R. Vaughan. 1985. Movements of white-tailed deer in Shenandoah National Park, Virginia. Annual Conference of the Southeast Association of Fish and Wildlife Agencies 39:396-402.
- Townsend, D.S., and A.D. Meyer. 2002. Rapid recovery of witch hazel (*Hamamelis virginiana* L.) by sprouting, following release from white-tailed deer (*Odocoileus virginianus* Zimm.) browsing. Natural Areas Journal 22:290-295.
- USDA, NRCS. 2004. The PLANTS Database, Version 3.5. National Plant Data Center, Baton Rouge, La. Available online http://plants.usda.gov>.
- Vellend, M. 2002. A pest and an invader: whitetailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). Natural Areas Journal 22:230-234.
- Vellend, M., J.A. Myers, S. Gardescu, and P.L. Marks. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. Ecology 84:1067-1072.

- Vickery, R.K., Jr., D.R. Phillips, and P.R. Wonsavage. 1986. Seed dispersal in *Mimulus* guttatus by wind and deer. The American Midland Naturalist 116:206-508.
- Waller, W.M., and W.S. Alverson. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25:217-226.
- Ward, J.S., and G.R. Stephens. 1995. Protection of tree seedlings from deer browsing. Pp. 507-514 *in* Proceedings of the 10th Central Hardwood Forestry Conference. General Technical Bulletin NE-197, U.S. Department of Agriculture, Forest Service, [Radnor, Pa.]
- Webster, C.R., M.A. Jenkins, and G.R. Parker. 2001. A field test of herbaceous plant indicators of deer browsing intensity in mesic hardwood forests of Indiana. Natural Areas Journal 21:149-158
- Willson, M.F. 1986. Avian frugivory and seed dispersal in eastern North America. Current Ornithology 3:223-279.
- Willson, M.F. 1993. Mammals as seed-dispersal mutualists in North America. Oikos 67:159-167.