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A Pest and
an Invader:
White-tailed Deer
(*Odocoileus
virginianus* Zimm.)
as a Seed Dispersal
Agent for
Honeysuckle Shrubs
(*Lonicera* L.)

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ABSTRACT: Predicting and managing the spread of invasive plant species require a sound and detailed knowledge of dispersal mechanisms. I examined white-tailed deer (*Odocoileus virginianus* Zimm.) feces in five mature forest stands in central New York, USA, and found seeds of alien invasive bush honeysuckles (*Lonicera tatarica* L., *L. morrowii* A. Gray, *L. × bella* Zabel) in feces from all five stands. *Lonicera* seeds were found in 66 of 72 pellet groups examined, and the overall mean number of seeds per pellet group was 62 ± 19 SE; within-stand means ranged from 0.6 ± 0.3 SE to 334 ± 165 SE. Percent germination of seeds collected in feces from one site was 76%, compared to 81% for fresh-collected seeds, and *Lonicera* seedlings were observed growing out of feces in the field. Prior to this study, the only important dispersers recognized for invasive *Lonicera* spp. have been birds. Using data from the literature on the feeding, digestive, and movement behaviors of deer vs. birds, I show that white-tailed deer have tremendous potential for contributing to the spread of invasive honeysuckles and perhaps other plant species.

Una Peste y un Invasor: Ciervo de Cola Blanca (*Odocoileus virginianus* Zimm.) como Agente Dispersante de Semillas del Arbusto Madreselva (*Lonicera* L.)

RESUMEN: La predicción y el manejo de plantas invasoras requiere un profundo y detallado conocimiento de sus mecanismos de dispersión. Examiné heces del ciervo de cola blanca (*Odocoileus virginianus* Zimm.) en cinco lotes de bosque maduro en el centro de New York, USA, y encontré semillas de madreselva (*Lonicera tatarica* L., *L. morrowii* A. Gray, *L. × bella* Zabel), un arbusto exótico invasivo en heces de los cinco lotes. Se encontraron semillas de *Lonicera* en 66 de las 72 muestras examinadas, y el número medio general de semillas por muestra fue 62 ± 19 SE; las medias dentro de cada lote variaron de 0.6 ± 0.3 SE a 334 ± 165 SE. El porcentaje de germinación de las semillas colectadas de las heces de un sitio fue 76%, comparado con el 81% de las semillas frescas, y se encontró que plántulas de *Lonicera* estaban creciendo de las heces en el campo. Previo a este estudio, los únicos dispersores importantes reconocidos de la invasiva *Lonicera* spp. eran los pájaros. Con datos de la literatura en la alimentación, digestión y conductas de movimiento de los ciervos vs. los pájaros, muestro que el ciervo de cola blanca tiene un gran potencial de contribución en la distribución de la madreselva y tal vez de otras especies de plantas.

Index terms: invasive species, *Lonicera*, mixed hardwood forest, seed dispersal, white-tailed deer

INTRODUCTION

Knowledge of dispersal mechanisms is essential for understanding and managing the spread of invasive species (Williamson 1996). For exotic plant species with adaptations for dispersal by animals, establishment of novel interactions with resident animal species is a prerequisite for subsequent invasion into natural areas. Despite the critical importance of such positive interactions, the subject has received relatively little attention in the invasion biology literature (Richardson et al. 2000). Even if one seemingly dominant mode of dispersal has been identified, additional dispersal modes may exist, and consideration of all possible ways in which seeds are dispersed is necessary for accurately predicting invasion dynamics (Allen et al. 1991).

In the temperate zone, birds and omnivorous mammals are considered the most

important seed dispersers for plants with fleshy fruits (Willson 1986, 1993). The role of large herbivores in seed dispersal is thought to be largely confined to plants with small, dry fruits and seeds (Janzen 1984), though Willson (1993) provided some examples of large herbivores (e.g., caribou, *Rangifer tarandus* L., and cattle, *Bos taurus* L.) dispersing seeds of fleshy-fruited species. In eastern North America, the dominant large herbivore is the white-tailed deer (*Odocoileus virginianus* Zimm.), which has increased dramatically in abundance in recent years, often causing severe damage to native forest plants through overbrowsing (Russell et al. 2001). Little is known about white-tailed deer as seed dispersers, but given their high densities and daily movements of up to a kilometer or more (Marchinton and Hirth 1984), there is great potential for deer to disperse seeds.

Several species of alien invasive honeysuckle are currently of concern in eastern North America, including the shrubs *Lonicera tatarica* L., *L. morrowii* A. Gray., their hybrid *L. × bella* Zabel, and *L. maackii* (Rupr.) Maxim., and the vine *L. japonica* Thunb. Several studies have suggested that honeysuckle invasion may inhibit forest regeneration and native plant diversity (Woods 1993, Luken and Thieret 1996, Hutchinson and Vankat 1997, Luken et al. 1997). Furthermore, Gould and Gorchov (2000) experimentally demonstrated negative effects of honeysuckle invasion on native plants. Frugivorous birds are assumed to be the only seed dispersers for invasive honeysuckles, apart from the possibility of seed predators (e.g., deer mice, *Peromyscus maniculatus* Wagner) dispersing small numbers of seeds (Williams et al. 1992). In this paper, I document the importance of white-tailed deer as dispersal agents for bush honeysuckles. In addition, I address the implications of such dispersal for honeysuckle invasions, and discuss the potential for synergistic effects of invaders and pests on native communities.

METHODS

The native ranges of *Lonicera tatarica* and *L. morrowii*, in western and eastern Asia, respectively, do not overlap. In their introduced ranges, the two species frequently produce hybrids (*L. × bella*), and it is often not possible to consistently distinguish the three taxa (Batcher and Stiles 2000). Seeds

of the three taxa were not distinguishable in this study, and the taxa are henceforth simply referred to as *Lonicera*.

In five mature mixed-hardwood forest stands near Ithaca, New York, USA, I collected a total of 72 white-tailed deer pellet groups. In one stand, McGowan's Woods, I collected 1 to 7 pellet groups on eight different days (33 total) in July and August 2000, and in the four additional stands (as well as McGowan's Woods), I collected 6 to 10 pellet groups across two different dates per stand in July 2001 (Table 1). Stands were selected independently of local *Lonicera* abundance. At two stands (Trillium Woods and Novak Woods; see Table 1), no *Lonicera* were observed in the vicinity; at the other three stands *Lonicera* was common around the stand edges, as is typical in central New York. No native *Lonicera* species were observed in or around any of the stands, and each stand was separated from all others by at least 9 km.

Pellet groups were individually washed in a 0.5-mm sieve, and all *Lonicera* seeds were manually retrieved and counted. Seeds obtained from McGowan's Woods in 2000 were transferred to moistened filter paper in petri dishes and stratified at 4°C for 13 to 16 weeks before germination trials. On 25 July 2000, fresh fruits of *Lonicera* from at least 10 shrubs at McGowan's Woods were also collected and washed, with two plates of 50 seeds

prepared as above. All stratified seeds were placed in a growth chamber and exposed to daily cycles of 15 hours of light (10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) at 25°C and 9 hours of darkness at 15°C for germination trials. Seeds were checked twice weekly for germination for four months.

RESULTS AND DISCUSSION

Lonicera seeds were found in white-tailed deer feces from all five stands, and in 66 of the 72 pellet groups. Within-stand means ranged from 0.6 ± 0.3 SE to 334 ± 165 SE seeds per pellet group, with an overall mean of 62 ± 19 SE (Table 1). Percent germination of seeds retrieved from feces at McGowan's Woods was 76%, compared to 81% for fresh-collected seeds. Stands with *Lonicera* common in the vicinity (McGowan's Woods, Schoolhouse Hill, and Bundy Road) had higher mean seeds per feces than other stands (Table 1).

To date, birds are the only important dispersal vectors reported for seeds of invasive honeysuckles in North America (Nuzzo and Randall 1997, Batcher and Stiles 2000). The results of this study clearly demonstrate that white-tailed deer also disperse viable *Lonicera* seeds. In addition, *Lonicera* seedlings have been observed growing out of white-tailed deer feces in the field (Figure 1; Jonathan Myers, Department of Ecology and Evolutionary Biology, Cornell University, unpubl. data), demonstrating that seedlings

Table 1. Descriptive statistics for *Lonicera* seeds found in feces of white-tailed deer collected near Ithaca, New York, USA.

Site	Year	Range of Dates of Collection	# Pellet Groups	Proportion of Pellet Groups with <i>Lonicera</i> Seeds	Seeds per Pellet Group		
					Mean \pm SE	Minimum	Maximum
McGowan's Woods	2000	20 July–12 Aug.	33	0.97	42 ± 7	0	150
McGowan's Woods	2001	23–31 July	10	0.90	48 ± 25	0	249
Schoolhouse Hill	2001	19–25 July	7	1.00	334 ± 165	1	1087
Bundy Road	2001	9–27 July	6	1.00	34 ± 11	1	82
Trillium Woods	2001	12–18 July	9	1.00	4.5 ± 1.5	1	12
Novak Woods	2001	13–27 July	7	0.43	0.6 ± 0.3	0	2
Overall			72	0.92	62 ± 19	0	1087

can become established from seeds dispersed by white-tailed deer. While it is possible that seed predators remove some seeds from feces, consumption of *Lonicera* seeds by seed predators is likely to be minimal (Williams et al. 1992). To determine the potential relative importance of white-tailed deer vs. birds as dispersal agents for exotic honeysuckles, I evaluated three lines of evidence. First, do white-tailed deer in other parts of the species' range ingest invasive *Lonicera* fruits? Second, how does the quantity of seeds dispersed by white-tailed deer compare to the quantity dispersed by birds? Finally, how widely can deer be expected to disseminate seeds relative to birds?

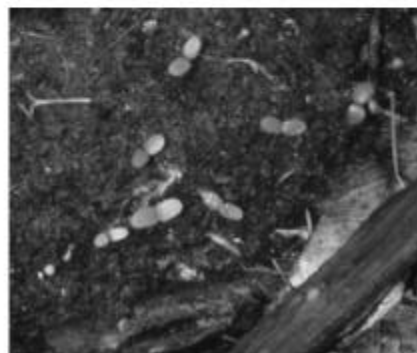


Figure 1. *Lonicera* seedlings growing out of white-tailed deer feces in a mature hardwood forest stand at Six Mile Creek, Ithaca, New York; this site is 3 km southwest of McGowan's Woods. (Photograph by Jonathan Myers, Department of Ecology and Evolutionary Biology, Cornell University)

Deer Feeding on *Lonicera* spp.

Lonicera spp. have been identified as important components of white-tailed deer diets in the northeast (Martin et al. 1951; this study), the southeast (Harlow and Hooper 1972), and parts of the midwestern United States (Torgerson and Porath 1984). For all of the invasive *Lonicera* spp. in North America, fruits are borne in the axils of relatively small leaves (6–8 cm long). Therefore, browsing of leaves and twigs while *Lonicera* is in fruit is likely to result in seed ingestion. Harlow and Hooper (1972) reported *Lonicera* fruits (probably *L. japonica*) in deer rumens from the southeast, and though they did not record seeds in a separate category, it is likely that seeds were present. I expect that white-tailed

deer ingest and disperse invasive *Lonicera* seeds in much of eastern North America.

Quantity of Seeds Dispersed

Comparing the quantity of seeds dispersed by different animals is made difficult by the patchiness of seed deposition, and by spatial and temporal variation in seed production, animal abundance, and the availability of alternative food items. Nonetheless, by making a few assumptions, one can make rough calculations of the relative quantities of honeysuckle seeds dispersed by deer and by birds.

Based on stand means of 0.6 to 334 *Lonicera* seeds per pellet group, and an average of 13 pellet groups per deer per day (Eberhardt and van Etten 1956), a single deer would disperse between 7 and > 4000 seeds per day during the period of honeysuckle fruiting. Current estimates of white-tailed deer density range up to 15 deer km⁻² in agricultural areas, and over 50 deer km⁻² in some suburban areas (Halls 1984). In the Ithaca, N.Y., area, current densities range from about 20 to 40 deer km⁻² (Paul Curtis, Department of Natural Resources, Cornell University, pers. com.). With a conservative estimate of 20 deer km⁻², and a period of seed dispersal lasting at least two months (Jonathan Myers, unpubl. data), white-tailed deer can disperse a cumulative total of 0.01 to 5.2 *Lonicera* seeds m⁻² during a growing season at a given forest stand in the Ithaca area. Site-to-site variation in the quantity of seeds dispersed by deer is probably related to the local abundance of honeysuckles.

Three published studies report quantitative, area-based estimates for seed deposition of invasive *Lonicera* spp. by birds. In a 15-year-old successional pine forest in Illinois, Smith (1975) found no seeds of *L. tatarica* during the first year of study, and 0.3 seeds m⁻² in the second year. In New Jersey, McDonnell and Stiles (1983) found no seeds of *L. japonica* deposited in traps in a recently abandoned field and 0.1 seeds m⁻² in a shrubby old field. When seed traps were placed directly under natural or artificial perch sites in fields, McDonnell and Stiles (1983) and McDonnell (1986) found 0.3 and 0.7 seeds of *L. japonica*

m⁻² in two different years. It is possible that fruit consumption and seed deposition by birds is higher in other regions and at other times. For example, fall-ripening fruits (e.g., *L. japonica*, *L. maackii*) may be consumed in large quantities by migrating flocks of birds, resulting in both a larger contribution of birds to seed dispersal, and a diminished role for deer if fruits are largely depleted. However, a comparison of my estimate for deer (0.01 to 5.2 seeds m⁻²) to those currently available for birds (0 to 0.7 seeds m⁻²) strongly suggests that white-tailed deer are important contributors to seed dispersal of invasive honeysuckles.

Following passage through bird digestive tracts, increased percent germination of nonstratified *Lonicera tatarica* seeds relative to controls occurs, but there is no difference for stratified seeds (Krefting and Roe 1949). Slightly reduced percent germination of deer-dispersed seeds (76%) relative to controls (81%) in the current study does not alter the conclusion that deer are important dispersal agents for invasive *Lonicera* seeds.

Long-Distance Dispersal

The distance a seed is dispersed by an animal depends on the amount of time the seed is retained in the digestive tract, and how far the animal travels during that time. Fecal deposition of food from a deer digestive tract begins about 15 to 20 hours following ingestion, peaks after 1 to 2 days, and may continue for a week or more (Mautz and Petrides 1971, Van Soest 1994). During periods of a few days, white-tailed deer typically travel within a range spanning about 1 km, and often much farther (Marchinton and Hirth 1984). During spring and summer, yearling males may disperse greater than 10 km, and in northern regions, autumn migrations of over 50 km are known to occur (Marchinton and Hirth 1984). Fruits of *Lonicera x bella*, *L. tatarica*, and *L. morrowii* ripen in summer with few fruits persisting into autumn; fruits of *L. maackii* and *L. japonica* ripen in autumn. It is almost certain that white-tailed deer routinely disperse seeds up to a kilometer from parent plants, and potentially much farther.

At least 20 bird species feed on honeysuckle fruits, including many songbirds (e.g., cedar waxwing, *Bombycilla cedrorum* Vieillot, and American robin, *Turdus migratorius* L.) and a few larger species (e.g., turkey [*Meleagris gallopavo* L.] and ruffed grouse [*Bonasa umbellus* L.], Ruesink 1998). For fruits with high water content (i.e., *Lonicera* spp., Ingold and Craycraft 1983), songbirds may pass seeds in as little as 15 to 20 minutes after ingestion; larger birds may retain seeds for up to several days (Welty and Baptista 1988). During the summer breeding season, territorial songbirds spend much of their time in an area of less than 1 ha; nonterritorial and premigratory birds may range up to 1 km or more (Welty and Baptista 1988). During autumn migrations, several bird species feed on *Lonicera* fruits (Suthers et al. 2000), and at a flight speed of 30 to 40 km h⁻¹ (Berthold 1993) may carry seeds up to 10 km in 15 minutes, or potentially much farther if retention time is protracted. However, individual birds are likely to carry only a few seeds at a time (Suthers et al. 2000). Both deer and birds can disperse seeds of invasive honeysuckles widely.

Pest and Invader

Overbrowsing by white-tailed deer, and competition from invasive honeysuckles, both inhibit regeneration of forest trees and negatively affect understory plants. If deer activity renders plant communities more invulnerable via reduced cover of native species, and simultaneously adds invasive plant seeds, the effects of deer and honeysuckles may in fact be synergistic rather than simply additive. However, the degree to which browsing by deer also has negative effects on honeysuckles is currently unknown, and the balance of interactions among deer, invasive honeysuckles, and native forest plants merits further study. Given the ubiquity of white-tailed deer in eastern North America, and their generalist diet, they potentially play an important role in dispersing seeds of a wide range of plant species.

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Mark Vellend is a doctoral candidate at Cornell University. He is interested in the dynamics of populations and communities in fragmented landscapes.

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