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Seed dispersal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*), by white-tailed deer in a fragmented agricultural-forest matrix

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Abstract

Ungulates are potentially important seed dispersers for many invasive plant species. While our understanding of which invasive plant species are dispersed by ungulates has improved over the last decade, the factors influencing this process remain poorly understood. To address this, we explored white-tailed deer (*Odocoileus virginianus*) seed consumption and dispersal of an invasive shrub (*Lonicera maackii*) in fragmented agricultural-forest matrices in western Ohio. In a pairwise browse preference experiment, deer browsed at similar levels on branches of *L. maackii* with fruits removed and fruits intact (mean ± 95% CI: 57±14% and 62±14%, respectively). We found no evidence that white-tailed deer disperse *L. maackii* seeds along an invasion front, but 31% of deer pellet groups collected in an invaded area contained germinable *L. maackii* seeds (maximum number of germinable seeds = 30). By combining hourly movement data specific to fragmented landscapes and gut retention time data, we projected that female deer disperse 91% of ingested seeds further than 100m from seed sources (i.e. long-distance seed dispersal), and rarely disperse seeds up to 7.9 km. We conclude that white-tailed deer can be important long-distance seed dispersal vectors of *L. maackii*, and that invader abundance and/or patch connectivity likely influence patterns of seed dispersal by white-tailed deer.

Key Words: deer browse, nearest neighbor, patch size, seed shadow projection

Seed dispersal represents the single point in many plants' life cycle where an individual can move. The movement of seeds allows plants to escape density-dependent mortality near parent plants (Janzen 1970), colonize new habitats (Clark et al. 1998), exchange genetic material across populations (Excoffier et al. 2009), and rescue populations from local extinction in metapopulation dynamics (Cain et al. 2000). Large-scale anthropogenic changes, such as invasion of exotic plant species and habitat fragmentation, are altering seed dispersal of many plant species, which has potentially negative consequences for conservation of plant populations and communities (McConkey et al. 2012). Invasive plant species represent an ideal system to study seed dispersal, especially along invasion fronts, and are of practical importance since dispersal is a critical step in the invasion pathway. Dispersal patterns are inferred by describing the proportion of seeds in discrete distance classes away from parent plants ("seed shadows", Clark et al. 2005). An alternative approach to inferring seed shadows involves combining short-scale vector movement and retention time data to project seed shadows (Murray 1988; Vellend et al. 2003). In order to project a seed shadow, three things must be understood: the agents responsible for dispersing seeds (dispersal vectors), the time period over which these vectors can carry seeds (retention time), and vector movement patterns on the same time scale as retention time. Seed shadow projections provide valuable insight into the importance of a dispersal vector by providing expectations of the most frequent (mean, median, or mode) and longest (maximum) dispersal distances a seed might experience.

Seed dispersal vectors that transport seeds over long distances, potentially connecting disjunct populations of plant species, are especially important to understand. Increasingly, suitable habit is undergoing fragmentation due to anthropogenic land-use changes, as is the case for forests in many parts of North America (Heilman and Strittholt 2002; Riiters et al. 2012).

North American ungulates, such as white-tailed deer (*Odocoileus virginianus*), disperse seeds through endozoochory (ingestion and defecation of viable seeds). Since ungulates have long gut retention times and potentially large daily movements, ungulate endozoochory occurs over long distances, and can potentially link fragmented habitat patches (Eycott et al. 2007; Jaroszewicz et al. 2013). Using seed shadow projection based on gut retention times and daily movement, Vellend et al. (2003) showed that white-tailed deer can disperse *Trillium grandiflorum* seeds > 3km away from seed sources in deciduous forests. As generalist herbivores, white-tailed deer consume a wide range of plant types during different seasons, including woody browse, forbs, crops, and grasses (Hewitt 2011). White-tailed deer browsing during fruit production can result in ingested seeds, and germinable seeds from dozens of native and exotic species have been found in white-tailed deer fecal pellets from North American temperate broadleaf forests (Myers et al. 2004; Williams and Ward 2006; Blyth et al. 2013). Since white-tailed deer abundance throughout eastern North America has increased relative to pre-colonial abundances (Rooney 2001), it is possible that increased access to long-distance seed dispersal vectors has facilitated the success of many ungulate-dispersed plant species.

We investigated the potential role of white-tailed deer as a seed dispersal vector for invasive shrubs in their introduced range by studying the relationship between white-tailed deer and Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder, Caprifoliaceae). Establishment of *L. maackii* alters native plant population dynamics (Gould and Gorchov 2000; Gorchov and Trisel 2003; Miller and Gorchov 2004), community composition (Collier et al. 2002; Hartman and McCarthy 2008; Christopher et al. 2014), and ecosystem functions (Arthur et al. 2012; McNeish et al. 2012). Propagule pressure and movement of dispersal vectors are important for the spread of this invasive shrub. *Lonicera maackii* presence in fragmented forest patches is negatively correlated with both distance from the nearest town and the amount of surrounding cropland (Bartuszevige et al. 2006; Gorchov et al. 2014a). Several bird species act as important seed dispersal vectors by consuming the bright red fruits produced by this shrub (Ingold and Craycroft 1983; Bartuszevige and Gorchov 2006). White-tailed deer are also likely *L. maackii* seed dispersal vectors, as 68% of the *L. maackii* seeds from the fecal pellets of captive deer fed fruit of this shrub were viable (Castellano and Gorchov 2013). Also, pellets collected from free-ranging white-tailed deer contained seeds of other invasive *Lonicera* species (Myers et al. 2004; Williams and Ward 2006). Here, we investigate the hypothesis that white-tailed deer are important seed dispersal vectors for invasive shrubs. To do this, we tested two predictions: 1) free-ranging white-tailed deer consume ripe *L. maackii* fruit, and 2) free-ranging white-tailed deer disperse germinable *L. maackii* seeds. Our results suggest white-tailed deer can be important seed dispersal vectors of this invasive shrub, but this importance likely depends on invader abundance and landscape connectivity, among other factors.

Methods

Study Areas

White-tailed deer foraging and seed dispersal data were collected at two sites in western Ohio, reflecting areas with high and low *L. maackii* abundance. The high *L. maackii* abundance ("invaded") site was the Miami University Ecology Research Center (ERC) (39° 31' 57" N, 84° 43' 23" W), Butler County. The ERC is a 93-ha property, with interspersed patches of forest, old fields, and row crops. *Lonicera maackii* was introduced to the area more than 50 years ago, and is now common in forest patches throughout the county (Hutchinson and Vankat 1997). *Lonicera maackii* is one of the most common plants at the ERC, both within forest stands and along edges (Pfeiffer and Gorchov 2015).

The low *L. maackii* abundance (“invasion front”) site was located 50-70 km north of the invaded site (40° 05’ 36” N, 84° 46’ 47” W) in Darke County (Figure 1). This site covered 23 km^2 of agricultural matrix with interspersed forest patches, agricultural fields, and residential housing. Agricultural fields predominantly contained corn and soy grown as row crops. Some forest patches had sparse abundance of *L. maackii* and other invasive plant species, but *L. maackii* was not present in most forest patches. A region of isolated forest patches approximately 15 km southeast of this study area was initially invaded by *L. maackii* about 20 years ago (Gorchov et al. 2014a). Today, established *L. maackii* populations are common in that region, as well as forest patches between it and the invasion front site (PWG, personal observation), defining this study area as a *L. maackii* invasion front. The discrete forest patches and low *L. maackii* abundance made this site well-suited to determine the ability of this invasive shrub to invade new areas through long-distance seed dispersal by white-tailed deer.

Hourly white-tailed deer movement data were collected from GPS-collared white-tailed deer between 2002 and 2006 in an agricultural-forest matrix in southern Illinois (37° 42’ 24” N, 89° 9’ 47” W). *Lonicera maackii* is present and established throughout this study area, although its abundance has not been determined. No browse preference or seed dispersal data were collected from this area. More data on land use and white-tailed deer distribution in the Illinois study area can be found in Storm et al. (2007).

Browse Preference Experiment

We conducted a pairwise browse preference experiment at the invaded site from October 2012 to January 2013, in order to monitor white-tailed deer browse on *L. maackii* stems while testing for preference between shrubs with and without fruit. We only included *L. maackii* growing on the forest edge for this experiment because (1) this high-light environment produces a higher fruit set compared to forest interiors, ensuring that enough fruit was present on the *L. maackii* stems to enable a perceivable treatment effect, and (2) white-tailed deer use forest edge habitat extensively (Stewart et al. 2011).

We distinguished two age classes of stem tissue: twigs and branches. Stems produced in the current year and bearing leaves were classified as twigs. Older stems, bearing multiple twigs but no leaves were classified as branches. Branches generally consisted of more woody tissue than twigs. On each of the 90 shrubs in this experiment, we monitored new white-tailed deer browse on a single horizontal branch, including all twigs borne on the branch. In order to control for factors that potentially confound white-tailed deer browse preferences (shrub age, size, or reproductive status), we only observed *L. maackii* branches that were between 1 and 2m above the ground, with ≥10 twigs (a proxy for branch size) and ≥10 fruits.

The 90 individual shrubs were divided into 45 pairs, and each pair consisted of two *L. maackii* 5 – 10 m apart. Shrub pairs were ≥100 m apart, to ensure independence of browse observations. In order to detect white-tailed deer browse preference between fruiting and non-fruiting *L. maackii* branches, each branch within a pair was randomly assigned one of two treatments: control or fruit removal. Control branches were left with fruits unaltered. Fruit removal branches had all fruit on the branch manually removed, along with any fruits within 0.5 m of the branch, in order to create a treatment effect large enough to be perceived by white-tailed deer.

Prior to the start of the experiment, we marked each target branch with an inconspicuous white string towards the proximal end of the branch. White-tailed deer browse, which is distinct from other browse (Swift and Gross 2008), was only measured distal to this point on the branch. We found it appropriate to distinguish between two types of white-tailed deer browse marks in this experiment: small browse marks on individual twigs (“twig browse”) and larger browse marks on branches with concurrent disappearance of one or more previously existing twigs (“branch browse”). The incidence of both browse types on *L. maackii* branches was recorded at the beginning and end of the experiment, and the difference between the two represented the amount of new white-tailed deer browse. We determined the proportion of branches in each treatment that experienced new white-tailed deer browse, and used the normal approximation to the binomial to develop 95% confidence intervals for each proportion.

We used a sign test to investigate whether deer preferred to browse on *L. maackii* branches with fruits intact. A sign test determines if the proportion of trials where a specific outcome occurs is significantly different from 0.5. If a *L. maackii* with fruits intact had a greater amount of new white-tailed deer browse than its paired *L. maackii* with fruits removed, this was considered preference for *L. maackii* with fruit. In cases where both branch and twig browse were observed within shrub pair, the direction of preference was assigned based on branch browse alone, since individual twigs that were browsed separately may have been missing entirely after branch browse. Pairs with lost flagging (n = 3) were excluded from analysis.

Seed Dispersal Observation

In order to determine the extent of *L. maackii* seed dispersal by white-tailed deer, we collected white-tailed deer fecal pellet groups from our study areas during the late fall and early winter. Initially, we opportunistically collected white-tailed deer pellet groups at the invaded site in December 2012 and January 2013. Due to the high abundance of *L. maackii* in this study area, our study design made it impossible to determine the source of any seeds found within fecal pellets.

In order to quantify the role of white-tailed deer in the spread of invasive shrubs to new areas, a more rigorous approach was taken the following year. Within the invasion front site, we located the closest *L. maackii* seed sources to our collection areas. Individual shrubs were considered reproductive if flowers were present in spring 2013. We identified two potential seed source populations, and recorded each individual's GPS coordinates. One population, located on the north end of the study area, consisted of several reproducing individuals near a pine (*Pinus* spp.) forest. A second population, located on the south end of the study area, consisted of two large individuals growing in a hedge row in high-light conditions. We chose forest patches neighboring these seed sources as collection areas, where reproducing *L. maackii* was either absent or found in abundances low enough to facilitate manual removal of shrubs. Forest patches were closed-canopy, secondary growth mixed deciduous forests, and ranged in size from 1.5 to 9 ha. Each had a history of logging, and white-tailed deer hunting was permitted throughout the study area. We established 10 collection areas, seven of which had reproducing *L. maackii* (range: 1 to 13) which were manually removed in June 2013. Removal of reproducing shrubs ensured that any *L. maackii* seeds found in collected white-tailed deer pellets were dispersed over long distances from other forest patches.

We collected white-tailed deer fecal pellets along transects in each collection area at the invasion front site. The GPS coordinates of each corner of the collection areas were used to establish two 100 m east-west transects per collection area, that were evenly spaced north-south throughout the forest patch. Each transect started at the forest edge, and extended into the forest interior. Every 10 m, we established a 2m x 10m subplot, centered on the transect. Transects were cleared of white-tailed deer pellets during the last week in September 2013, and fresh pellets were collected bi-weekly through the end of December 2013.

After collection, all pellets were cold stored at 5°C for six weeks before being transferred intact to sterile vermiculite, where they were kept at 24°C during the day and 15°C at night in a greenhouse, representing conditions favorable for *L. maackii* germination (Hidayati et al. 2000). Once samples were planted, seedling emergence was recorded weekly. In order to control for the unlikely event of contamination by other *Lonicera* seeds in the greenhouse, control pots, containing only sterile vermiculite, were used.

Seed Shadow Projection

In order to develop an expected distribution of seed dispersal distances for white-tailed deer endozoochory of an invasive shrub, we projected a seed shadow using existing gut retention time and movement data (Murray 1988; Vellend et al. 2003). Each of these data sets is described by a matrix. The matrix describing vector gut retention time provides the probability that a seed is passed out of the dispersal vector's intestinal tract during a given hour. It has a single column, and a number of rows (72) equal to the maximum retention time (in hours) for a seed. Forage quality affects gut retention time in mammals (Warner 1981), so we used gut retention data from a captive male white-tailed deer that was fed a diet of sumac (*Rhus typhina*) inflorescences (Mautz and Petrides 1971). This was a more appropriate analog to white-tailed deer browse on *L. maackii* than diets employed in other captive white-tailed deer gut retention studies (Jenks and Leslie 1989; Barnes et al. 1992). It is important to note that these data could differ from the retention times of free-ranging white-tailed deer, but we are not aware of any such studies. We estimated the retention time (X-axis) and cumulative percent of marker defecated (Y-axis) for each point in Figure 1 in Mautz and Petrides (1971). The distribution of retention times were fit to a lognormal distribution (Rawsthorne et al. 2009) using the MASS package in R (Venables and Ripley 2002). This lognormal distribution ($\mu = 3.38$, $\sigma = 0.35$) allowed us to calculate the probability density that a seed was defecated each hour. This approach showed that 26% of ingested material was egested after 24 hours, 93% was egested after 48 hours, and >99% was egested within 72 hours. Hence, we projected seed dispersal by white-tailed deer over 72-hour periods. We populated the retention time matrix with lognormal probability densities values for hours 1-72; these values summed to 0.997 so they did not require rescaling to constitute a probability distribution (which sums to 1).

The matrix describing a dispersal vector's hourly movement provides the probability that a vector is located in a discrete displacement class away from a starting point (rows) at hourly intervals (columns). We calculated Euclidean distance between each hourly position from the GPS-collared white-tailed deer. The dataset included hourly position data for 26 white-tailed deer between October and December, totaling over 39,000 point positions. All but one of the 26 white-tailed deer in the study were female, due to the original study's focus on overlap of doe home ranges (Kjaer et al. 2008). Fourteen white-tailed deer were adult females, one was an adult male, ten were female yearlings, and one was a female fawn. Female white-tailed deer in each age class had similar hourly movement patterns (Appendix A) and consequently were pooled for seed shadow projection. Details regarding study findings and capture methods from this dataset, including Institutional Animal Care and Use Committee approvals, are found elsewhere (Schauber et al. 2007; Storm et al. 2007; Kjaer et al. 2008; Anderson et al. 2011). We chose 6:00PM for the starting time of the 72-hour period, since white-tailed deer are often most active at this time (Roleau et al. 2002). Hourly displacement was summarized into 100 m distances classes (Vellend et al. 2003). The number of rows was the number of 100 m distance classes extended to the maximum displacement covered (in this case, 7.9 km). This displacement matrix thus had 79 rows and 72 columns.

The matrix describing hourly movement was multiplied by the matrix describing gut retention time to project a seed shadow, described by a single column matrix with 79 rows (one for each 100 m distance from the origin, Eqn. 1). Each element in this matrix describes the probability that a *L. maackii* seed is dispersed into the discrete displacement class.

Landscape configuration

We compared the landscape configurations of our three study areas to assess the applicability of the Illinois deer movement data to the Ohio landscapes where seed dispersal data were collected. In the case of the invaded area, where the collection area was small (<0.5 km), we collected landscape statistics in a 2 km buffer around the collection area. This represents an area large enough to properly describe the home range of white-tailed deer in an agricultural-forest matrix (Quinn et al. 2013). Land use in the study areas were classified as either forest patch or non-forest patch. Specifically, we compared forest patch area-weighted shape index, nearest neighbor, and patch area coefficient-of-variation, as well as road density in each study area, due to their influence on white-tailed deer movement (Ng et al. 2008; Walter et al. 2009).

Results

Browse Preference

We observed new white-tailed deer browse on the majority of *L. maackii* branches. Specifically, 62 ± 14% of *L. maackii* branches with fruits intact and 57 ± 14% of branches with fruits removed were browsed (95% confidence intervals). White-tailed deer browsed more on the fruiting branch in 55% of pairs, browsed more on the branch with fruits removed in 31% of pairs, browsed equally on both branches in 9% of pairs, and browsed on neither branch in 5% of pairs (Figure 2). Overall, there was no significant browse preference for branches with fruit over branches without fruit (number of trials = 42, $P = 0.64$).

Seed Dispersal Observation

From the 29 white-tailed deer pellet groups we collected from the invaded site in December 2012 and January 2013, *L. maackii* seedlings emerged from 9 pellet groups (31%), with an average of 2.5 ± 6.7 germinable seeds per collected pellet group (maximum = 30). The following year, we collected a total of 53 white-tailed deer pellet groups from the invasion front site between October and December 2013 and no *L. maackii* seedlings emerged (Table 1).

Seed Shadow Projection

The maximum displacement of a white-tailed deer within a 72-hour movement period was 7.9 km. A strikingly high proportion of seeds (91%) were projected to disperse >100m away from the seed source. The mode and median (50% cumulative probability) of our seed shadow projection showed that white-tailed deer are most likely to disperse seeds approximately 300 m from a seed source in fragmented landscapes. Seven percent of seeds were projected to disperse >1 km, and in extreme cases (0.3%) seeds were projected to disperse >7 km away from seed sources (Figure 3).

Landscape configuration

Forest patches were typically closest together in the invaded area (mean nearest neighbor = 55.3 ± 36.2 m), while forest patches in the invasion front had the most regular shapes (mean shape index = 2.55 ± 0.67) and the least variation in size (forest patch coefficient of variation = 180.7). Road density varied little among study areas (range 1.22 to 1.43 km km^{-2}, Table 2).

Discussion

In this study, we tested the importance of white-tailed deer as seed dispersal vectors of invasive shrubs. We found that white-tailed deer in an invaded area frequently browsed on *L. maackii* while fruits were ripe, providing an opportunity for seed ingestion and subsequent seed dispersal. We also found evidence of white-tailed deer dispersing *L. maackii* seeds in a heavily invaded area, but not along an invasion front, despite the presence of nearby seed sources. A projected seed shadow, which used habitat-specific movement data, suggests that white-tailed deer disperse *L. maackii* seeds over long distances in a landscape of forest fragments in an agricultural matrix.

Browse Preference

White-tailed deer frequently browsed on *L. maackii* in the invaded study area in the late fall and early winter, as new browse marks were observed on most branches. This pattern may be explained by *L. maackii* phenology, since this invasive shrub is frost-tolerant and retains its foliage into late fall unlike other common food sources in this region (Wilfong et al. 2009; Johnston et al. 2012). Dichromatic color vision in white-tailed deer may explain the lack of browse preference for fruiting *L. maackii* branches observed in this study. Many seed dispersal vectors, including many bird species, respond to chromatic signals (Schaefer 2006), such as the bright red colors found in *L. maackii* fruits. Accordingly, at least 12 species of birds in southwestern Ohio consume *L. maackii* fruits (Ingold and Craycroft 1983; Bartuszevige and Gorchov 2006). However, many mammalian herbivores, including white-tailed deer, have only two ocular cones, restricting the ability of these species to see colors in the red end of the visible spectrum (Ditchkoff 2011). While *L. maackii* fruits do not attract white-tailed deer in the same way they attract avian fruigvores, our work shows that white-tailed deer do consume ripe fruits while browsing *L. maackii* during late fall to early winter, providing an opportunity for white-tailed deer to disperse seeds of this invasive shrub.

White-tailed deer browse has been implicated as a major driver of population decline in some native plant species (Rooney and Waller 2003), but it often facilitates both invasive herbs and invasive shrubs (Eschtruth and Battles 2009; Knight et al. 2009). We present evidence that white-tailed deer browse can be widespread throughout a population of reproducing *L. maackii* (approximately 60% of observed shrubs had at least some woody tissue consumed). Our work, focused on the implication of white-tailed deer browse for seed dispersal, was not designed to assess the possible negative impacts of browse on population dynamics of invasive shrubs. However, other research shows that white-tailed deer browse can reduce recruitment of invasive shrubs. Near our invaded site, cover of *L. maackii* at heights from 0.5 to 1.5 m was significantly higher after four years of deer exclosure than in paired deer access plots (J. Peebles-Spencer and D. Gorchov, unpubl. data). Both recruitment of *L. maackii* and the combined diameter growth rate of four species of invasive shrubs (*L. maackii*, *Rosa multiflora*, *Berberis thunbergii*, *Ligustrum vulgare*) were higher in deer exclosures than ambient-density controls in Indiana (Shelton et al. 2014). The importance of deer browse on both invasive plant recruitment and seed dispersal is likely context-dependent, determined in part by the overall palatability of the plant community (Bee et al. 2011). It is not surprising that the invaded study area, which is dominated by unpalatable invasive shrubs, white-tailed deer browse on *L. maackii* is extensive.

Seed Dispersal

Seed dispersal of invasive *L. maackii* seeds by white-tailed deer was relatively common in the invaded study area (31% of pellet groups contained germinable *L. maackii* seeds). Our seed shadow projection indicated that white-tailed deer-dispersed seeds were likely traveling hundreds of meters, although our study design was unable to confirm this. This suggests that seed dispersal by white-tailed deer has potential importance for population dynamics and genetic structure in areas of high *L. maackii* abundance. *Lonicera maackii* populations in southwestern Ohio exhibit high levels of genetic diversity that suggest frequent long-distance seed dispersal among populations (Barriball et al. in press). Our results suggest that this genetic variation may partly be maintained through long-distance seed dispersal by white-tailed deer. Additionally, seed dispersal by white-tailed deer could rescue populations of *L. maackii* from eradication efforts by land managers, since long-distance seed dispersal has been shown to prevent local extinctions of populations undergoing metapopulation dynamics (Cain et al. 2000).

Despite collecting 53 white-tailed deer pellet groups at the invasion front site (a greater sampling effort than collection at the invaded area), no germinable *L. maackii* seeds were found. Germinable seeds from 13 plant species were contained within pellets (Guiden, unpublished data), indicating that our handling of pellets was not responsible for the lack of viable *L. maackii* seeds. Collection areas at the invasion front site ranged from approximately 500 m to 2100 m from the closest seed source. According to our seed shadow projection, 43% of *L. maackii* seeds consumed by white-tailed deer should have been dispersed over these distances. We conclude that seed dispersal by white-tailed deer is uncommon along an invasion front and not primarily responsible for the spread of this invasive shrub. Our finding that white-tailed deer are conditional seed dispersal vectors for *L. maackii* has implications for management of invasive plants and white-tailed deer. White-tailed deer dispersal of seeds is most important in areas where *L. maackii* is established. Although we did not detect seed dispersal by white-tailed deer at the invasion front, it is possible that in different contexts (e.g. more continuous forest habitat, more abundant seed sources) white-tailed deer could introduce *L. maackii* seeds to uninvaded habitat, and this potential should not be neglected.

There are two non-mutually exclusive explanations for the observed discrepancies in seed dispersal patterns between sites. The first involves white-tailed deer browse preference. White-tailed deer consumption and dispersal of *L. maackii* seeds (and perhaps seeds of other invasive species) is likely dependent on the relative abundance of the invasive plant. Where it establishes, *L. maackii* is associated with declines in forest herb, seedling, and sapling layers (Hartman and McCarthy 2008), which can constitute important elements of white-tailed deer diets (Vangilder et al. 1982; Johnson et al. 1995). As the abundance of preferred food sources declines, large herbivores should increase consumption of less preferred plant species (van Beest et al. 2010), such as *L. maackii*. Differences in white-tailed deer densities could achieve the same effect: a higher density of consumers could result in decreased availability of preferred food sources, and hence more consumption of less preferred *L. maackii*. Pellet count surveys suggest that white-tailed deer abundance was lower at the invasion front (Guiden 2014) than the invaded study are (Crist, unpublished data), but different analyses were used to reach these conclusions, making direct comparisons speculative. If this invasive shrub continues to spread within the invasion front, or white-tailed deer densities increased dramatically, we would expect increased *L. maackii* consumption and seed dispersal.

Alternatively, idiosyncrasies in landscape configuration, such as patch connectivity, shape, and size can affect white-tailed deer movement (Walter et al. 2009, Williams et al. 2011). Forest patches in the invaded area were more connected (lower mean distance between nearest neighboring forest patch), while forest patches in the invasion front were more condensed (less perimeter per area) and more variable in size (larger coefficient of variation). All else being equal, we expect fewer long movements by white-tailed deer at the invasion front in our study, and therefore less seed dispersal between disjunct forest patches. This highlights the need to account for differences in landscape configuration when comparing patterns of seed dispersal in different areas.

Our seed shadow projection builds upon the understanding of seed dispersal by white-tailed deer described in Vellend et al. (2003)'s seed shadow projection of *T.grandiflorum* by only using movement data collected in a fragmented landscape at the time of *L. maackii* fruit ripening. The mode of projected dispersal distances were similar (300m), but our seed shadow projection shows a much greater maximum dispersal distance (7.9 km vs. 3.9 km; Vellend et al. 2003). This suggests that seasonality and landscape configuration, factors known to influence white-tailed deer movement, could consequently alter the long-distance seed dispersal capacity of white-tailed deer. To explore how seed dispersal by male deer might differ from that projected for females, we used the movement data from the single male white-tailed deer in our movement data set, and the same gut retention data, to project a seed shadow. The mean seed dispersal distance for the male white-tailed deer (900m, Guiden unpublished data) was approximately three times further than the projected median seed dispersal distance for female white-tailed deer (300m), which is consistent with existing knowledge of white-tailed deer behavior (Nixon et al. 1991, Walter et al. 2009). This could suggest that when seed dispersal vectors have strong sexual dimorphism, including many ungulate species, the contributions of each sex to seed dispersal merits consideration.

While the ecological consequences of white-tailed deer herbivory have been well studied over the past several decades (reviewed by Côté et al. 2004), less is known about the causes and consequences of native and invasive plant seed dispersal by white-tailed deer. Reports of exotic species seed dispersal by white-tailed deer are becoming increasingly common in the literature (Vellend 2002; Myers et al. 2004; Williams and Ward 2006), highlighting the complex interactions between white-tailed deer and plant communities. Since North American white-tailed deer abundances have increased dramatically since pre-colonial times (Rooney 2001), understanding how seed dispersal by white-tailed deer has contributed to the spread of invasive plants will be an important aspect to consider when planning eradication and control of these plant species. Our study demonstrates the need to shift efforts beyond compiling lists of plant species that are dispersed by white-tailed deer to a more mechanistic understanding of how ecological context impacts seed dispersal by white-tailed deer.

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References

Anderson CW, Nielsen CK, Storm DJ, Schauber EM (2011) Modeling habitat use of deer in an exurban landscape. Wildl Soc Bull 35:235–242.

Arthur MA, Bray SR, Kuchle CR, McEwan RW (2012) The influence of the invasive shrub, *Lonicera maackii*, on leaf decomposition and microbial community dynamics. Plant Ecol 213:1571–1582.

Barnes TG, Varner LW, Blankenship LH, Gallagher JF (1992) Indigestible particulate passage in white- tailed deer. In: Brown RD (ed) The Biology of Deer. Springer-Verlag, New York pp. 436–442.

Barriball, K., E.J. McNutt, D.L. Gorchov, and O.J. Rocha. In press. Inferring invasion patterns of *Lonicera maackii* (Rupr) Herder (Caprifoliaceae) from the genetic structure of 41 naturalized populations in a recently invaded area. Biol Invasions.

Bartuszevige AM, Gorchov DL (2006) Avian seed dispersal of an invasive shrub. Biol Invasions 8:1013–1022.

Bartuszevige AM, Gorchov DL, Raab L (2006) The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. Ecography 29:213–222.

Bee JN, Tanentzap AJ, Lee WG, Lavers RB, Mark AF, Mills JA, Coomes DA (2011). Influence of foliar traits on forage selection by introduced red deer in New Zealand. Basic Appl Ecol 12:56–63.

Blyth LH, Ouborg LJ, Johnson DM, Anderson LJ (2013). The short-term germination and establishment success of deer-dispersed seeds in mesic temperate forests. J Torrey Bot Soc 140:334–348.

Cain M, Milligan B, Strand A (2000) Long-distance seed dispersal in plant populations. Am J Bot 87:1217–1227.

Castellano SM, Gorchov DL (2013) White-tailed deer (*Odocoileus virginianus*) disperse seeds of the invasive shrub, Amur honeysuckle (*Lonicera maackii*). Nat Areas J 33:78–80.

Christopher CC, Matter SF, Cameron GN (2014) Individual and interactive effects of Amur honeysuckle (*Lonicera maackii*) and white-tailed deer (*Odocoileus virginianus*) on herbs in a deciduous forest in the eastern United States. Biol Invasions 16:2247–2261.

Clark J, Fastie C, Hurtt G, Jackson ST, Johnson C, King GA, Lewis M, Lynch J, Pacala S, Prentice C, Schpp EW, Webb III T, Wyckoff P (1998) Reid's paradox of rapid plant migration. Bioscience 48:13–24.

Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86:2684–2694.

Collier M, Vankat J, Hughes M (2002) Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. Am Midl Nat 147:60–71.

Côté SD, Rooney TP, Tremblay JP, Dussault C, Waller DM. (2004) Ecological impacts of deer overabundance. Annu Rev Ecol Evol Syst 35:113–147.

Ditchkoff SS (2011) Anatomy and physiology. In: Hewitt DG (ed) Biology and Management of White-tailed Deer. CRC Press, Boca Raton pp. 75-105.

Eschtruth AK, Battles JJ (2009) Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conserv Biol 23:388–99.

Excoffier L, Foll M, Petit RJ (2009) Genetic consequences of range expansions. Annu Rev Ecol Evol Syst 40:481–501.

Eycott AE, Watkinson AR, Hemami MR, Dolman PM (2007) The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. Oecologia 154:107–18.

Gorchov DL, Henry MC, Frank P (2014a) Invasion of an exotic shrub into forested stands in an agricultural matrix. Invasive Plant Sci and Manag. 7: 336-344.

Gorchov, DL Castellano SM, Noe DA. (2014b) Long-distance dispersal and diffusion in the invasion of *Lonicera maackii*. Invasive Plant Sci and Manag. 7:464–472.

Gorchov D, Trisel D (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecol 166:13–25.

Gould A, Gorchov D (2000) Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. Am Midl Nat 144:36–50.

Guiden PWG (2014) The role of white-tailed deer (*Odocoileus virginiana*) in long-distance seed dispersal of Amur honeysuckle (*Lonicera maackii*). Master thesis, Department of Biology, Miami University, Oxford OH, USA.

Hartman K, McCarthy B (2008) Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). J Torrey Bot Soc 135:245–259.

Heilman G, Strittholt J (2002) Forest fragmentation of the conterminous United States: assessing forest intactness through road density and spatial characteristics. Bioscience 52:411–422.

Hewitt DG (2011) Nutrition. In: Hewitt DG (ed) Biology and Management of White-tailed Deer. CRC Press, Boca Raton pp. 75-105.

Hidayati SN, Baskin JM, Baskin CC (2000) Dormancy- breaking and germination requirements of seeds of four *Lonicera* species (Caprifoliaceae) with underdeveloped spatulate embryos. Seed Sci Res 10: 459–469

Hutchinson TF, Vankat JL (1997) Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conserv Biol 11:1117–1124.

Ingold J, Craycroft M (1983) Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. Ohio J Sci 83:256–258.

Janzen D (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528.

Jaroszewicz B, Pirożnikow E, Sondej I (2013) Endozoochory by the guild of ungulates in Europe's primeval forest. For Ecol Manag 305:21–28.

Jenks J, Leslie D (1989) Digesta retention of winter diets in white-tailed deer (*Odocoileus virginianus*) fawns in Maine, USA. Can J Zool 67:1500–1504.

Johnson A, Hale P, Ford W (1995) White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. Am Midl Nat 133:18–25.

Johnston S, Henry M, Gorchov D (2012) Using advanced land imager (ALI) and landsat thematic mapper (TM) for the detection of the invasive shrub *Lonicera maackii* in southwestern Ohio forests. GIScience Remote Sens 49:450–462.

Kjær LJ, Schauber EM, Nielsen CK (2008) Spatial and temporal analysis of contact rates in female white-tailed deer. J Wildl Manag 72:1819–1825.

Knight TM, Dunn JL, Smith LA, Davis JA, Kalisz A (2009) Deer facilitate invasive plant success in a Pennsylvania forest understory. Nat Areas J 29:110–116.

Mautz W, Petrides G (1971) Food passage rate in the white-tailed deer. J Wildl Manag 35:723–731.

McConkey KR, Prasad S, Corlett RT, Campos-Arceiz A, Brodie JF, Rogers H, Santamaria L (2012) Seed dispersal in changing landscapes. Biol Conserv 146:1–13.

McNeish RE, Benbow ME, McEwan RW (2012) Riparian forest invasion by a terrestrial shrub (*Lonicera maackii*) impacts aquatic biota and organic matter processing in headwater streams. Biol Invasions 14:1881–1893.

Miller KE, Gorchov DL (2004) The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139:359–75.

Murray KG (1988) Avian seed dispersal of three neotropical gap-dependent plants. Ecol Monogr 58:271–298.

Myers JA, Vellend M, Gardescu S, Marks PL (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.

Ng J, Nielson C, Clair CS (2008) Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. Hum Wildl Confl 2:34-47.

Nixon C, Hansen L, Brewer P, Chelsvig J (1991) Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildl Monogr 18:1-77.

Pfeiffer SS, Gorchov DL (2015) Effects of the Invasive Shrub *Lonicera maackii* on soil water content in eastern deciduous forest. Am Midl Nat 173:38–46.

Quinn ACD, Williams DM, Porter WF (2013) Landscape structure influences space use by white-tailed deer. J Mammal 94:398–407.

Rawsthorne J, Roshier DA, Murphy SR (2009) A simple parametric method for reducing sample sizes in gut passage time trials. Ecology 90:2328–31.

Riitters KH, Coulston JW, Wickham JD (2012) Fragmentation of forest communities in the eastern United States. For Ecol Manag 263:85–93.

Rooney TP (2001) Deer impacts on forest ecosystems: a North American perspective. Forestry 74:201–208.

Rooney TP, Waller DM (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. For Ecol Manag 181:165–176.

Rouleau I, Crete M, Ouellet JP (2002) Contrasting the summer ecology of white-tailed deer inhabiting a forested and an agricultural landscape. Ecoscience 9:459–469.

Schaefer HM (2006) The role of chromatic and achromatic signals for fruit detection by birds. Behav Ecol 17:784–789.

Schauber E, Storm D, Nielsen C (2007) Effects of joint space use and group membership on contact rates among white-tailed deer. J Wildl Manag 155–164.

Shelton AL, Henning JA, Schultz P, Clay K (2014) Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. For Ecol Manag 320:39–49.

Stewart KM, Boyer RT, Weisberg PJ (2011) Spatial use of landscapes. In: Hewitt DG (ed) Biology and Management of White-tailed Deer. CRC Press, Boca Raton pp. 75-105.

Storm DJ, Nielsen CK, Schauber EM, Woolf A (2007) Space use and survival of white-tailed deer in an exurban landscape. J Wildl Manag 71:1170–1176.

Swift CE, Gross MK (2008) Preventing deer damage. Colorado State Univ. Extension (http://www.ext.colostate.edu).

van Beest FM, Mysterud A, Loe LE, Milner JM (2010) Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. J Anim Ecol 79:910–22.

Vangilder L, Torgerson O, Porath W (1982) Factors influencing diet selection by white-tailed deer. J Wildl Manag 46:711–718.

Vellend M (2002) A pest and an invader: white-tailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). Nat Areas J 22:230–234.

Vellend M, Myers JA, Gardescu S, Marks PL (2003) Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. Ecology 84:1067–1072.

Venables WN, Ripley B D (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Walter WD, VerCauteren KC, Campa H, Clark WR, Fischer JW, Hygnstom SE, Mathews NE, Nielsen CK, Schauber EM, Van Deelen TR, Winterstein SR (2009) Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. Landsc Ecol 24:1405–1420.

Warner A (1985) Rate of passage of digesta through birds and mammals. Nutr Abstr Rev Ser B 51:789–820.

Wilfong BN, Gorchov DL, Henry MC (2009) Detecting an invasive shrub in deciduous forest understories using remote sensing. Weed Sci 57:512–520.

Williams DM, Dechen Quinn AC, Porter WF (2011) Landscape effects on scales of movement by white-tailed deer in an agricultural–forest matrix. Landsc Ecol 27:45–57.

Williams SC, Ward JS (2006) Exotic seed dispersal by white-tailed deer in southern Connecticut. Nat Areas J 26:383–390.

Table 1 A total of 82 white-tailed deer pellet groups were collected at two sites to investigate the potential for deer to disperse *Lonicera maackii* seeds. Only pellet groups collected at the invaded area contained germinable *L. maackii* seeds.

	Invaded Area	Invasion Front
Deer pellet groups collected	29	53
Deer pellet groups containing germinable *Lonicera maackii* seeds	9	0
Mean *Lonicera maackii* seeds per pellet group (± 1 standard deviation)	2.5 ± 6.7	0

Table 2 Forest patch and landscape characteristics that influence white-tailed deer movement and seed dispersal. Characteristics are compared across three study areas where white-tailed deer movement ("Movement Data") or seed dispersal data ("Invasion Front" and "Invaded Area") were collected.

	Movement Data	Invasion Front	Invaded Area
Location	Illinois	Ohio	Ohio
Lonicera maackii abundance	Low	Low	High
Area-weighted Shape Index	9.38 ± 1.97	2.55 ± 0.67	8.99 ± 2.10
Nearest neighbor (m)	124.2 ± 181.3	214.3 ± 189.6	55.3 ± 36.2
Patch area coefficient-of-variation	423.9	180.7	354.1
Road Density (km km^{-2})	1.22	1.36	1.43

Figure Captions

Figure 1 Map of Darke County, Ohio study area, showing forest patches where white-tailed deer pellets were collected (dark gray) and surrounding land use (Forest: light gray, Crops: hatch, Residential: white, Road: black). Two *L. maackii* seed sources (black circles) in the landscape are also shown. Forest patches southeast of this landscape also contained reproducing *L. maackii*.

Figure 2 White-tailed deer preference among 42 pairs of *L. maackii* shrubs assigned to fruit removal treatments and control treatments (fruits left intact). Within each pair, the shrub with more woody tissue consumed by white-tailed deer was considered to be preferred.

Figure 3 Projected seed shadows for dispersal of *L. maackii* seeds by 25 female white-tailed deer. Bars represent the probability that a *L. maackii* seed will be dispersed to each 100 m distance class. The median and mode of projected seed dispersal distances was 300 m away from a seed source, but rarely seed dispersal was projected to occur up to 7900 m away from a seed source. Minor tic marks represent 200 m intervals.

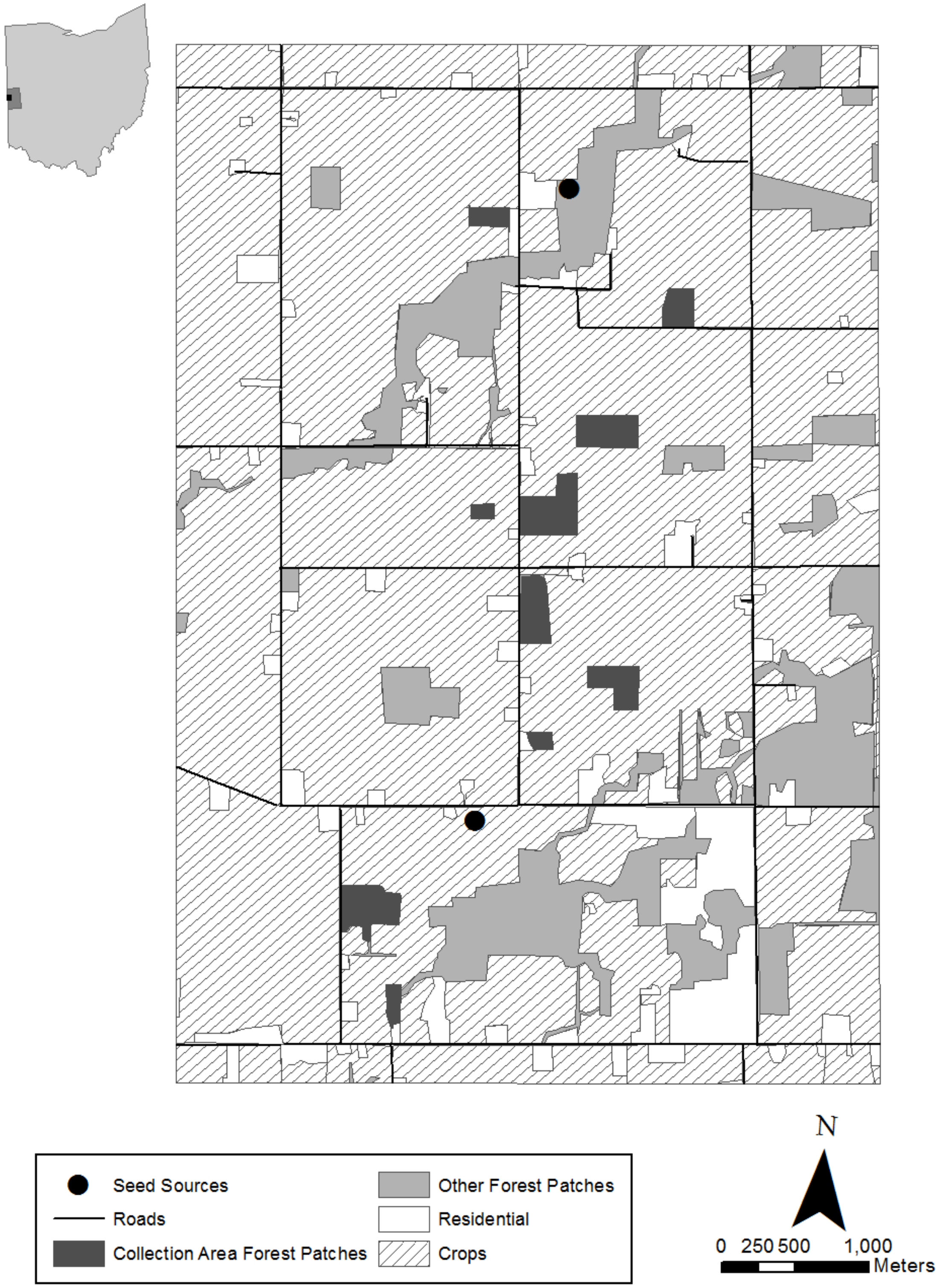
Seed Sources
Roads
Collection Area Forest Patches
Other Forest Patches
Residential
Crops
N
0 250 500 1,000
Meters

Figure 1

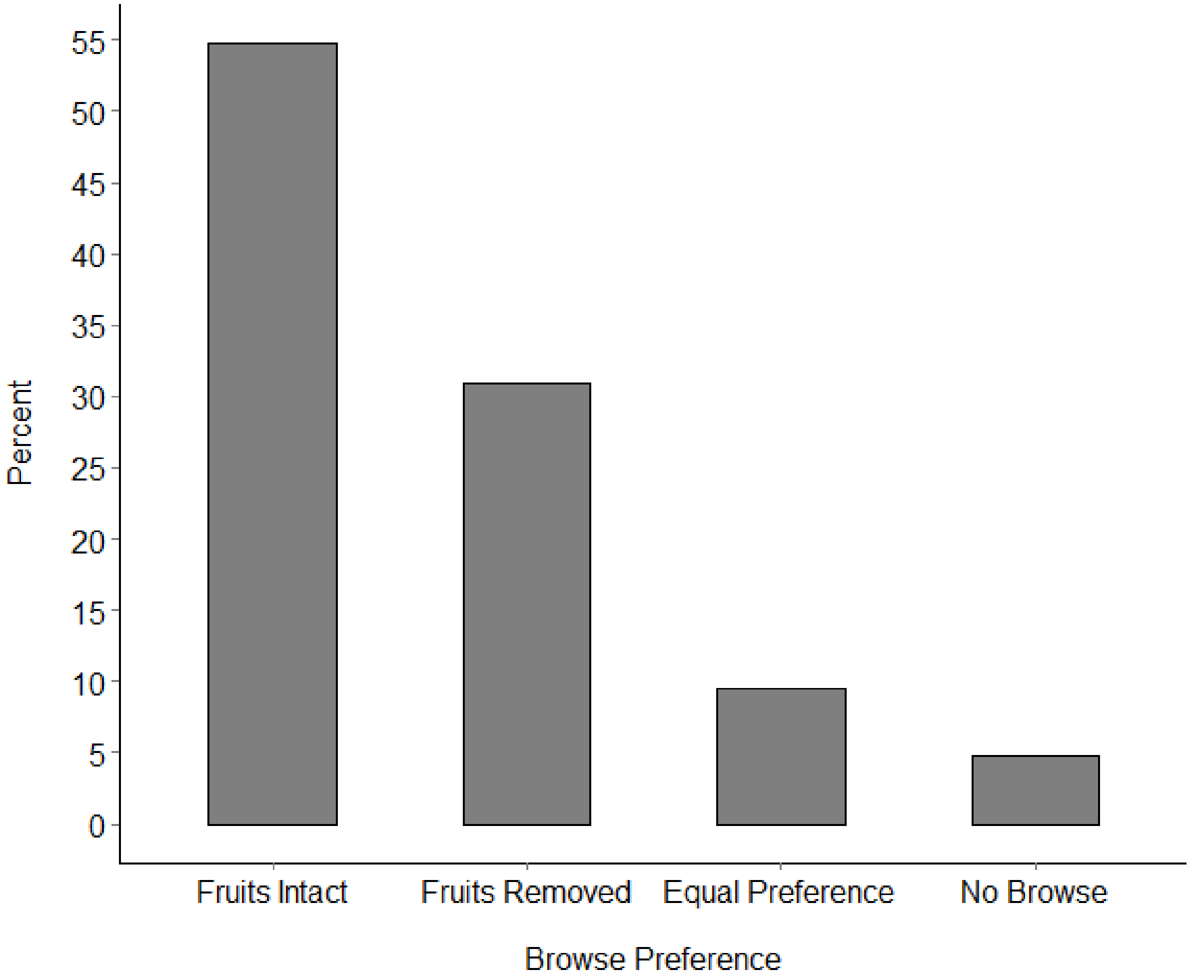
Percent
55
50
45
40
35
30
25
20
15
10
5
0
Fruits Intact
Fruits Removed
Equal Preference
No Browse
Browse Preference

Figure 2

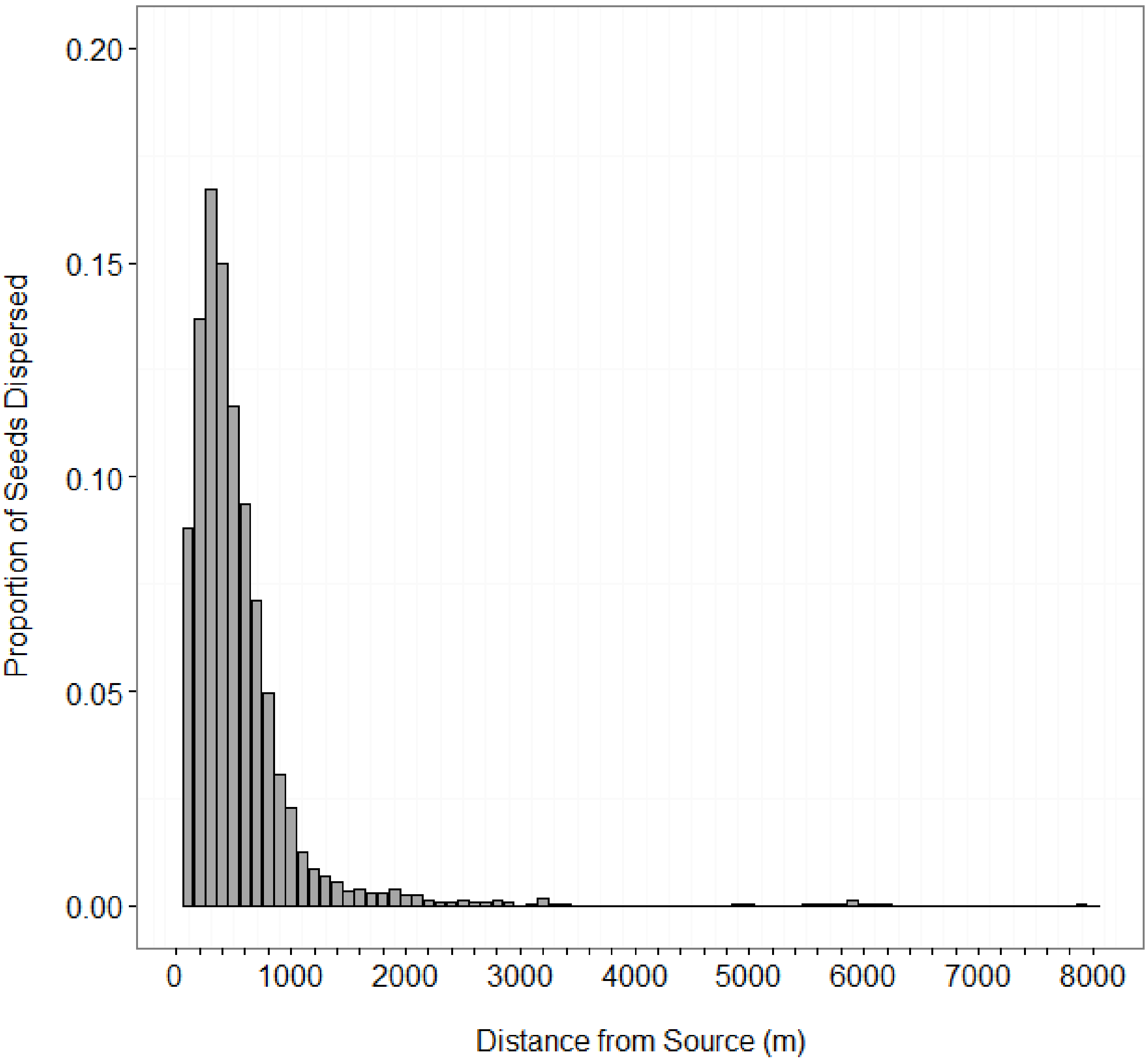
0.20
0.15
0.10
0.05
0.00
Proportion of Seeds Dispersed
0
1000
2000
3000
4000
5000
6000
7000
8000
Distance from Source (m)

Figure 3

Appendix A

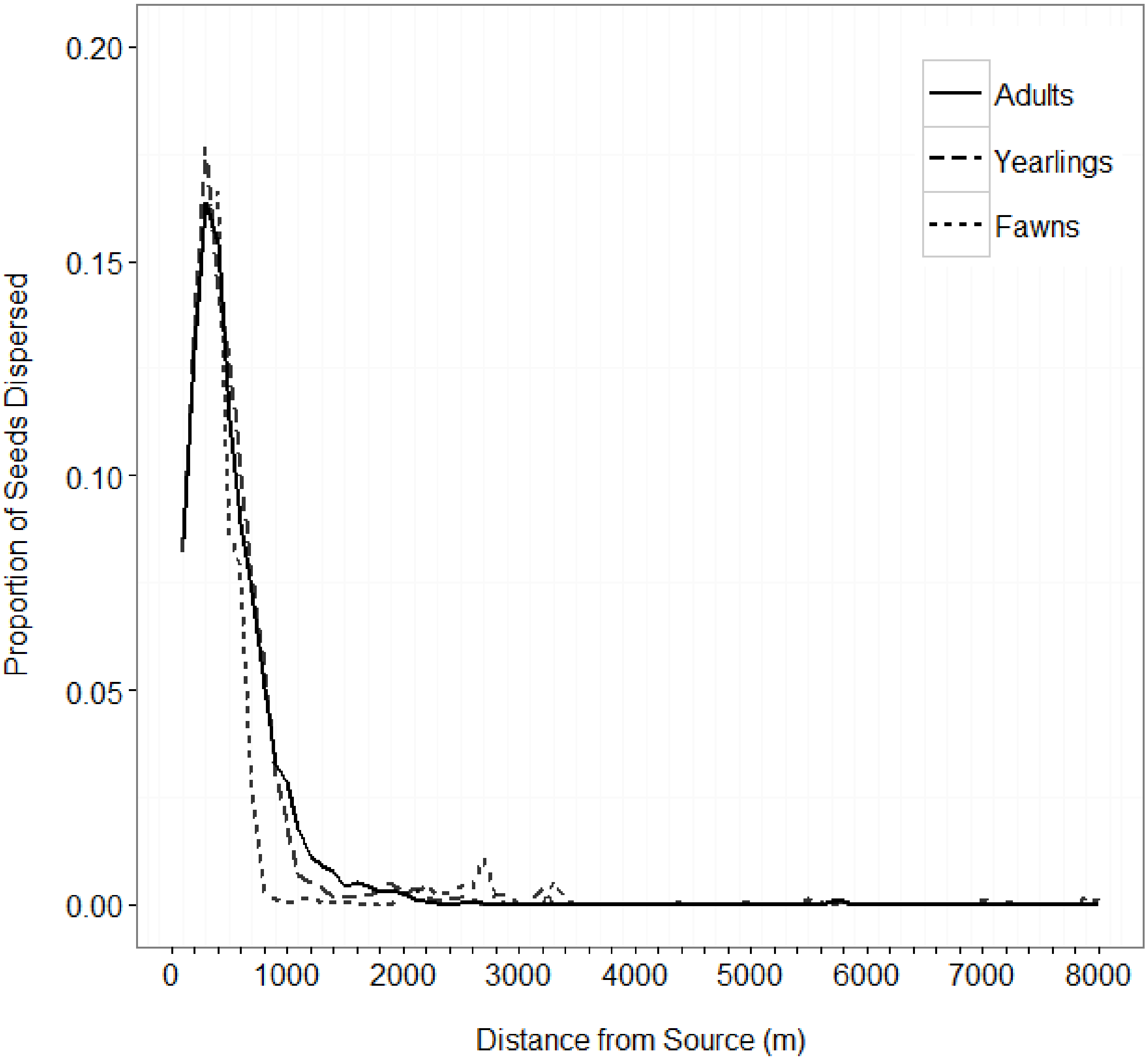

Fig A1: Seed shadows projections for deer separated by age class, including fawn (n=1), yearling (n=8), and adults (n=16). Minor tic marks represent 200 m intervals.