ABSTRACT

THE ROLE OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN LONG-DISTANCE SEED DISPERsal OF AMUR HONEYSUCKLE (*LONICERA MAACKII*)

by Peter W. Guiden

Long-distance seed dispersal contributes to the spread of invasive plants. Identification of seed dispersal vectors will help manage the spread of invasive plants, such as *Lonicera maackii*, a common invasive shrub in Ohio. Several bird species are dispersal vectors of *L. maackii*, but recent evidence suggests that deer may also contribute. I found that deer browse on *L. maackii* while fruits were ripe, but did not prefer fruiting branches. Male deer were projected to disperse a greater proportion of seeds over long distances than female deer. I found no evidence of deer dispersal of *L. maackii* seeds along an invasion front, but 31% of deer pellet groups collected in an invaded area contained germinable *L. maackii* seeds. I conclude that deer are important long-distance seed dispersal vectors of *L. maackii*, and suggest that land managers interested in eradicating this invasive shrub reduce the number of male deer in local herds.
THE ROLE OF WHITE-TAILED DEER (ODOCOILEUS VIRGINIANUS) IN LONG-DISTANCE SEED DISPERSAL OF AMUR HONEYSUCKLE (LONICERA MAACKII)

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Introduction

The rapid introduction and spread of invasive plant species is one of the most prominent environmental changes of our time, impacting both ecological systems and human societies. Invasion by non-native plant species often causes the extinction of native plant species at the local scale (Powell et al. 2013), and can induce dramatic changes in multi-species interactions, such as pollination (Schweiger et al. 2010). Invasive plant species can also interfere with ecosystem functioning, such as nutrient cycling (Ehrenfeld 2010; Vila et al. 2011). Non-native plants can reduce beneficial ecosystem services (Pejchar and Mooney 2009), and their removal and control cost billions of dollars every year in the US alone (Pimentel et al. 2005). Consequently, invasive plant species are one of the foremost threats to ecological integrity of natural areas.

Understanding the seed dispersal capacity of invasive plants makes it possible to develop models projecting the spread of a given invasive species. In order to do this, we must understand three things. First, we need to understand what vectors are responsible for dispersing a species’ seeds, since these vectors have distinct movement patterns. Primarily wind-dispersed seeds often have dispersal patterns distinct from primarily animal-dispersed seeds (Le Galliard et al. 2012). A plant’s dispersal ability can be further complicated by having secondary or even tertiary dispersal vectors (Dennis & Westcott 2007). Second, we need to understand how long these vectors can carry seeds (retention time). This can range between several minutes and several days, depending on the vector (Rawesthorne et al. 2009), resulting in different distributions of dispersal distances. Third, we need to understand vector movement patterns over a seed’s retention time. Wind-dispersed seeds are likely to move predominantly in one direction with prevailing winds, whereas animal-dispersed seeds are more likely to move in complex patterns around a seed source, depending on factors influencing animal behavior. Identifying and describing dispersal vectors of invasive plants is just the first step in truly understanding patterns in seed dispersal, since each vector is likely to react differently to large-scale anthropogenic changes, such as habitat fragmentation and climate change (McConkey et al. 2012).

Dispersal events are often classified into short- or long-distance dispersal. Short-distance dispersal is a diffusion process that enables a plant to spread within a stand, whereas long-distance dispersal enables a plant to establish in new habitats and recolonize previously occupied disjunct habitats (Sakai et al. 2001). Long-distance dispersal events are relatively rare, but are critical for rapid spread of a plant species across a landscape (Clark et al. 1998). Patterns of long-distance dispersal are often inferred by describing seed shadows and fitting dispersal kernels to them (Clark et al. 2005). An alternative approach sometimes used in the study of animal-mediated seed dispersal, involves combining short-scale vector movement and retention time data to project seed shadows (Murray 1988; Vellend et al. 2003). Seed shadows provide insight into patterns of long-distance seed dispersal, including both mean and maximum dispersal distances, and can be especially helpful in projecting dispersal patterns for animal vectors that move over long distances. When the relationship between plant and dispersal vector is well-understood, it is possible to develop spatially-explicit models of invasive species spread (Merow et al. 2011). This can in turn help tailor management policies toward areas that are at greater risk for invasion.
One important seed dispersal vector in eastern North America is the eastern white-tailed deer (*Odocoileus virginianus*). While the ecological consequences of deer herbivory have been well studied over the past several decades (reviewed by Côte et al. 2004), including the facilitation of invasive plant species through selective browsing on native plant species (Knight et al. 2009), less is known about precisely how deer disperse seeds of native and invasive plant species. As generalist herbivores, deer consume a wide range of plant types during different seasons and in different parts of their geographic range, including woody browse, forbs, crops, and grasses (Hewitt 2011).

However, the fate of native and invasive seeds consumed by deer is not well understood. Deer act as seed predators for some species, completely destroying consumed seeds (Furedi and McGraw 2006), while dispersing the seeds of other species intact (Vellend 2002). Germinable seeds of 72 plant taxa, including 46 exotic species were recovered from deer fecal pellets in central New York, (Myers et al. 2004). Similar results were found in southern Connecticut, where 86 plant taxa were recovered, including 40 exotic species (Williams and Ward 2006). Invasive plant species are found in higher abundance near deer trails compared to plots located 3m away from deer trails, suggesting that deer dispersal of these species can impact the distribution of plants (Lefcort and Pettoello 2012).

While it is clear that deer disperse the seeds of invasive species, it is less clear what patterns of deer dispersal look like. The relatively large body size and movement capacity of deer indicates a potential to disperse seeds over long distances. Projected seed shadows for deer dispersal of the understory herb *Trillium grandiflorum* indicate that deer may disperse seeds over 3km (Vellend et al. 2003), and it is likely that deer could disperse seeds of some invasive plant species over similar spatial scales. Since deer abundance has increased throughout eastern North America compared to pre-colonial abundances (McCabe and McCabe 1997), it is possible that the availability of this long-distance dispersal vector facilitated the spread of many invasive plant species.

I investigated the hypothesis that white-tailed deer are vectors for long-distance dispersal of Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder, Caprifoliaceae). *Lonicera maackii* is a prominent invasive shrub in eastern North America, and is listed as invasive/banned in Connecticut, prohibited in Massachusetts, and a noxious weed in Vermont (USDA PLANTS Database). At least part of this success may be explained by enemy release from native arthropod herbivores, as its leaves contain toxic compounds and it has minimal arthropod damage in its introduced range (Cipollini et al. 2008; Lieurance and Cipollini 2012). *Lonicera maackii* has the ability to drastically alter the composition of plant communities where it is found. Competition with this shrub negatively affects reproduction and survival of native annuals (Gould and Gorchov 2000), survival and growth of tree seedlings (Gorchov and Trisel 2003), and growth and reproduction of native perennial herbs (Miller and Gorchov 2004). At the community level, *L. maackii* is associated with decreased species richness and abundance of both tree and herbaceous species (Collier et al. 2002; Hartman and McCarthy 2008).

*Lonicera maackii* can also affect ecosystem functioning. Where it invades, this shrub accelerates nutrient cycling and increases nitrogen content of litter in terrestrial forest systems (Arthur et al. 2012). Additionally, *L. maackii* leaf litter inputs to headwater streams also elevate allochthonous nitrogen inputs and consequently alter the identity of stream macroinvertebrate communities (McNeish et al. 2012). The combined alterations of both community and ecosystem properties in its introduced range has led to serious concern about the impact of this exotic plant.
The phenology of *L. maackii* in part explains its success in its introduced range. This shrub leafs out before most other woody species, and retains its leaves later into winter (McEwan et al. 2009; Wilfong et al. 2009; Johnston et al. 2012). *Lonicera maackii* flowers in May and early June (McKinney and Goodell 2011), and produces fruit (red berries) that ripens in October and is removed by fruigory and abscision due to cold temperatures and precipitation through January (Bartuszevige et al. 2006b).

Understanding the ability of *L. maackii* to disperse over long distances is necessary in order to predict the location and type of habitats it will spread to in the future. This invasive shrub has successfully established widely across North America, from Texas to Ontario (USDA PLANTS Database), and undoubtedly its ability to disperse seeds has contributed to it attaining this wide distribution. *Lonicera maackii* presence in woodlots in southwest Ohio is negatively correlated with both distance from the nearest town and the amount of surrounding cropland, suggesting that propagule pressure and movement of dispersal vectors are important for the spread of this invasive shrub (Bartuszevige et al. 2006a; Gorchov et al. 2014). Birds are important *L. maackii* dispersal vectors, especially around forest edges. Robins retain *L. maackii* seeds up to 70 minutes, and are more likely to defecate seeds in woodlot spurs, edges, or corridors, despite the relatively low availability of these habitat types (Bartuszevige and Gorchov 2006).

Recent information suggests that deer also play a potentially large role in *L. maackii* dispersal. Deer pellets collected in central New York and southern Connecticut contained seeds of other invasive *Lonicera* species (Myers et al. 2004; Williams and Ward 2006). Castellano and Gorchov (2013) fed *L. maackii* fruit to a captive deer, and found that 68% of the seeds collected from the fecal pellets were viable. Deer gut retention times are as long as 65 hours (Mautz & Petrides 1971), much longer than bird gut retention times. Moreover, *L. maackii* bears fruit and retains its leaves during the late fall/early winter, making it an attractive food source at this time. Deer tend to have large home ranges, and therefore move over further distances during this season (Kjaer et al. 2008). Therefore, deer can potentially disperse seeds over very long distances relative to other species acting as dispersal vectors. In addition, they are known to frequent forest interiors at this time (Rouleau et al. 2002), which may complement avian seed dispersal of *L. maackii* around woodlot edges.

I hypothesize that deer play a key role in the long-distance seed dispersal of *L. maackii* through endozoochory. An assumption of this hypothesis is that deer ingest mature *L. maackii* fruits, which I tested by monitoring new deer browse on both fruiting and non-fruiting branches. I also make the following two predictions based on this hypothesis. First, I predict that a projected seed shadow for deer dispersal of *L. maackii* seeds will include seeds dispersed long-distances (>1km). Second, I predict that deer fecal pellets collected in woodlots with no reproducing *L. maackii* within 1 km will contain viable *L. maackii* seeds. Since these seeds by necessity originated outside the woodlot where they were collected, this would provide evidence of long-distance seed dispersal through deer. Together, support for these predictions would implicate deer as an important long-distance dispersal vector of invasive *L. maackii*, while improving our understanding of the adverse ecological effects of deer.
Study Areas

This study was conducted at two sites in western Ohio, reflecting areas with high and low *L. maackii* densities. The high *L. maackii* density (“invaded”) site was located at the Miami University Ecology Research Center (ERC) in Butler County, Ohio. The ERC is a 69-hectare property, with interspersed woodlots, agricultural fields, old fields, and mowed fields. *Lonicera maackii* was introduced to this landscape more than 50 years ago, and invasion is now common in woodlots throughout Butler County (Hutchinson & Vankat 1997; Bartuszevige et al. 2006a). *Lonicera maackii* is one of the most common plants at the ERC, both within forest stands and along edges (Pfeiffer and Gorchov, in press). Crist et al. (unpublished data) estimated white-tailed deer density at 11.2 deer km\(^{-2}\) in summer and 6.7 deer km\(^{-2}\) in winter, according to transect-based distance sampling of deer fecal pellets (Urbanek et al. 2012), while an aerial thermal imaging survey estimated a winter deer density of 3.9 deer km\(^{-2}\) (T. Millette, unpublished data).

The low *L. maackii* density (“invasion front”) site was located 50-70km north of the invaded site, in rural north-central Darke County, Ohio (40° 05’ 36” N, 84° 46’ 47” W to 40° 08’ 36” N 84° 48’ 01” W, Figure 1). This site covered 23 km\(^2\) of agricultural matrix with interspersed woodlots (occasionally up to 1.1km from the closest neighboring woodlot, Gorchov et al. in press) and residential housing. Agricultural fields predominantly contained corn and soy grown as row crops. Contrary to the invaded site, some woodlots had sparse cover of *L. maackii* and other invasive plant species, while *L. maackii* was absent from most woodlots. A landscape approximately 15km southeast of this study area was first invaded by *L. maackii* about 20 years ago, and most woodlots there now have small populations of this shrub (Gorchov et al. 2014). The fragmented landscape and low *L. maackii* cover made this site well-suited to study the long-distance dispersal of this invasive plant into uninvaded areas. Late fall and early winter deer density was estimated at 1.2 deer km\(^{-2}\) (Appendix 1).

Within the invasion front site, I determined where *L. maackii* was present and where it was absent. I classified woodlots within this study area as either “source woodlots” or “pellet survey woodlots”. Source woodlots contained reproducing *L. maackii* individuals. Reproductive status was assigned to *L. maackii* individuals that had flowers present in spring 2013 preceding this study. Once source woodlots in the area were identified, I chose neighboring woodlots as pellet survey woodlots. In these woodlots, reproducing *L. maackii* was either absent or found in low abundance. Of the ten pellet survey woodlots in this study area, seven had reproducing *L. maackii* which were manually removed in June 2013 (minimum=1 individual, maximum=13 individuals). Removal of reproducing shrubs ensured that any *L. maackii* seeds found in collected deer pellets were dispersed from other woodlots (i.e. over long-distances).
Methods

Browse Preference

In order to determine whether deer consume mature *L. maackii* fruits, and whether they browse preferentially on branches with mature fruit, I conducted a pairwise browse preference experiment at the invaded site from October 2012 to January 2013. I established 45 pairs of shrubs that were at least 100m apart to ensure independence of browse observations, using *L. maackii* throughout the entire ERC property. Each pair consisted of two *L. maackii* shrubs 5 - 10m apart. This distance ensured that individuals of a pair were close enough to each other to compare the amount of new deer browse between the shrubs, relative to other individuals in the study. I exclusively used *L. maackii* growing on the forest edge in this experiment, for two reasons. This high-light environment favors a high fruit set compared to forest interiors, ensuring that enough fruit was present on the *L. maackii* branches to make a dramatic treatment effect. A second justification of this criteria is that deer tend to use forest edges extensively, although not exclusively (Stewart et al. 2012).

For each shrub, I observed new deer browse on a single target branch. In order to control for difference among shrubs, I only chose *L. maackii* branches that were between 1 and 2m in height, had ≥10 twigs and ≥10 fruits. The branch height criterion avoided confounding deer browse with that of rabbits. Deer browse is distinct from other browse, since it leaves rough, shredded bark without teeth marks (Swift and Gross 2008). The twig number criterion was a proxy for branch size, since *L. maackii* has highly variable branch architecture; the amount of tissue available may affect a deer's propensity to browse on a certain branch.

At the beginning of the experiment (October 16, 2012), I marked each target branch with an inconspicuous white string towards the proximal end of the branch, in order to avoid influencing deer behavior. Deer browse was only measured distal to this point on the branch.

In order to detect deer browse preference between fruiting and non-fruiting *L. maackii* branches, each branch within a pair was randomly assigned one of two treatments. Control branches were left with fruits unaltered. Removal branches had all fruit on the target branch stripped off, along with any fruits within 0.5 m of focal branch. This was done so that the treatment effect was large enough to be perceived by deer, while the distance between shrubs (5 – 10m) was ample enough to avoid this removal of fruits from influencing deer browse on the control branch. I found it appropriate to distinguish between two types of browse in this experiment: twig browse and branch browse (Figure 2). Twigs were defined as current year stems bearing leaves. Branches were defined as older, twig-bearing stems that did not bear leaves. Generally, twigs were smaller than branches. The incidence of both branch browse and twig browse on each focal branch was recorded at the beginning (October 16, 2012) and end of the experiment (December 16, 2012).

The amount of new deer browse was calculated as the difference in deer browse incidence between December and October. I used a sign test to test the null hypothesis that both control and removal treatments were equally like to be preferred by browsing deer. Pairs whereflagging from one shrub was lost (n=3) were excluded from analysis. Pairs were assigned a value of “1” if the control *L. maackii* had a greater amount of new deer browse than its paired *L. maackii* with fruits
removed, and “-1” if the *L. maackii* with fruits removed had a greater amount of new deer browse than its paired control *L. maackii*. If there was equal amount of browse on paired individuals, a “0” was assigned; these pairs were excluded from the sign test, since these pairs gave no information about deer browse preference between control and removal treatments. In cases where both branch and twig browse were observed within a single pair of branches, 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. An assumption of this method is that the simultaneous consumption of multiple twigs and their supporting stem represents a greater preference than browse on twigs alone.

**Seed Shadow Projection**

In order to determine the specific contribution of deer endozoochory to seed dispersal of invasive *L. maackii*, I projected a seed shadow using existing gut retention time and daily movement data (Murray 1988; Vellend et al. 2003). These data are described by two matrices. The first matrix, describing gut retention time, represents the probability that a seed is passed out of a deer’s intestinal tract during a given hour. This matrix is a single column, with a number of rows equal to the number of hours in question. Deer diet used is an important consideration for seed shadow projections, since forage quality affects gut retention time in mammals (Warner 1981). I used gut retention data from a captive male deer that was fed a diet of sumac (*Rhus typhina*) inflorescences (Fig. 1 from Mautz and Petrides 1971), which was a more appropriate analog to deer browse on *L. maackii* than diets employed in other gut retention studies (Jenks and Leslie 1988; Barnes et al. 1992). The retention time (X-axis) and cumulative percent of marker defecated (Y-axis) for each point in this figure was estimated using a ruler. The percent of marker defecated at each retention time was determined by subtracting the previous point’s cumulative percent of marker defecated. These retention time data were then fit to a lognormal distribution, which accurately describes the positively skewed shape of gut retention time distributions (Rawesthorne et al. 2009). Fitting these gut retention time data to a lognormal distribution shows that in 72 hours, over 99% of ingested seeds will be egested, compared to 26% after 24 hours and 93% after 48 hours. Hence, a 72-hour time scale is appropriate to describe deer gut retention, and the matrix describing the probability of deer egesting seeds had 72 rows.

The second matrix, describing hourly movement of deer, represents the probability that a deer will be located in a given distance class from a starting point at one hour intervals, based on displacement (Euclidean distance). Hourly position data for this projection were obtained from GPS-collared deer in an agricultural-woodlot matrix in southern Illinois, which is similar in landscape structure to my study areas in southwest Ohio. Dr. Eric Schauber and Dr. Clay Nielsen originally recorded these data between 2002 and 2006, and agreed to collaborate with me for this research. The dataset included hourly position data for 26 deer between late September and the end of December, totaling over 39,000 hours of deer position data (Appendix 2). The maximum displacement of a deer within a 72-hour movement period was 7.9km. I chose 6:00PM for the starting time, since deer are most active at this time (Roleau et al. 2002). 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 72 columns, one for each hour of retention time. This makes the dimensions of this matrix 72 rows by 79 columns.
The matrix describing gut retention time was multiplied by the matrix describing hourly movement to project a seed shadow, described by a single column matrix, with 79 rows (one for each 100m distance from the origin). Each element in this matrix describes the probability that a *L. maackii* seed is dispersed into the corresponding displacement. This provides a theoretical expectation for white-tailed deer to disperse *L. maackii*, and allows us to determine the role that deer play in the long-distance dispersal of this invasive shrub.

I explored whether deer of different sexes produced distinct seed shadow projections, based on differences in their hourly movement patterns. All but one of the 26 deer in the study were female, due to the original study’s focus on overlap of doe home ranges (Kjaer et al. 2008). Fourteen deer were adult females, one was an adult male, ten were female yearlings, and one was a female fawn. Female deer in each age class had similar hourly movement patterns, and consequently were pooled for sex-specific seed shadow projection (Appendix 3). Bootstrap analysis was used to generate confidence intervals for the female seed shadow projection. I projected a seed shadow using four 72-hour movement periods for each of the 25 female deer, for a total of 100 72-hour movement periods. This process was repeated 10,000 times. This number of 72-hour movement periods was chosen in order to allow each deer to contribute equally, while maximizing the variation possible in each deer. The 250th and 9750th greatest value for each distance class was used to determine 95% confidence intervals. This analysis also allowed me to test for significant differences between male and female seed shadows. Bootstrap analysis was not used to describe uncertainties in male movement data, due to the very small number of male 72-hour movement periods (n=3). In this approach, the probability of observing a greater proportion of seeds dispersed over 1km from the seed source in a female-generated versus male-generated seed shadow represents the one-tailed p-value. R code for these seed shadow projections is provided in Appendix 4.

**Seed Shadow Observation**

In order to determine whether or not deer disperse *L. maackii* seeds *in situ*, I collected deer fecal pellet groups from both the invaded site and the invasion front study area during the late fall and assayed them for seedling emergence. At the invaded site I opportunistically collected 15 deer pellet groups on December 13, 2012 and 14 deer pellet groups on January 9-10, 2013. Due to the high abundance of *L. maackii* in this study site, it was impossible to determine which plant acted as the seed source.

This was not the case in the invasion front study area, where the positions of the sparse *L. maackii* seed sources were known. I collected deer fecal pellets from the fragmented woodlots located in the invasion front site to test the predictions made by the seed shadow projection. I identified two source woodlots, representing two populations of mature *L. maackii* in the study area (Figure 1). These populations were the closest potential seed sources. I recorded the GPS coordinates of all reproducing *L. maackii* individuals within the source woodlots. One population, located on the north end of the study area, consisted of several reproducing individuals near a remnant pine forest. The second population, located on the south end of the study area, consisted of two large individuals growing in a windbreak in high-light conditions.

Near these source woodlots, we established 10 pellet survey woodlots. Pellet survey woodlots were closed-canopy, secondary growth mixed deciduous forests, and ranged in size from
1.5 to 9ha. Each had a history of logging, and deer hunting was permitted throughout the study area. The coordinates of each corner of pellet survey woodlots were recorded with GPS and used to establish two 100m east-west transects per woodlot, that were evenly spaced north-south. Each transect started at the forest edge, and extended into the forest interior. Every 10m, I established a 20m² subplot, centered on the transect. Transects were cleared of deer pellets during the last week in September 2013, and fresh pellets were collected bi-weekly through the end of December 2013. Deer pellet surveys have been used to obtain estimates of deer population density (Eberhardt and van Etten 1956), so I used the total number of pellets collected over the course of the collection survey to estimate deer density in the study area (Appendix 1).

After collection, 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. These conditions promote *L. maackii* germination (Hidayati et al. 2000). Once samples were planted, seedling emergence was recorded weekly. Control pots, containing only sterile vermiculite, where used to ensure that samples were not contaminated by any other *Lonicera* seed sources in the greenhouse. *Lonicera maackii* seedlings are distinguishable from seedlings of other species due to their simple, opposite, ovate leaves which are covered with conspicuous fine trichomes when young. Additionally, a pilot study demonstrated that this method yields similar germination results compared to *L. maackii* seeds that are removed from deer pellets prior to planting (Appendix 5).

Multiple regression was used to determine what other factors affected the probability that deer pellets were found at both the woodlot and subplot scale. Several potential predictor variables, at both the woodlot and subplot level, were generated in Arc-GIS, version 10.1. Land use in this study area was classified as either woodlot, crop, or residential. Polygon shapefiles were constructed for each land use throughout the study area, and the perimeter and area of each collection woodlot shapefile was extracted. Shapefiles were rasterized, and the percent of each land use in 500m and 1000m buffers around woodlots and subplots was determined. I determined the distance of each woodlot and subplot to the closest *L. maackii* seed source and road, as well as the distance of each subplot to the closest woodlot edge.

At the woodlot level, I investigated the relationship of the number of deer pellet groups collected in a woodlot to 12 variables describing the study landscape. However, I anticipated correlation among these, so this list was pared by determining which pairs of variables had a correlation coefficient greater than 0.70 (Appendix 6). When two predictor variables were correlated, the variable that was better correlated with the response variable was retained. For woodlots, the retained predictors were size, shape (perimeter to area ratio, PAR), isolation (distance to the closest neighboring woodlot, McCollin 1993; Norris & Stutchbury 2001), distance to the nearest road, and percent cropland, residential land, and roads in 500m and 1000m buffers. With these variables, I used forward stepwise linear regression with AIC using the MASS package in R (Venables and Ripley 2002) to determine what variables best explained patterns in deer pellet deposition in the study area. The only unique variable at the subplot level was distance of each subplot to the woodlot edge. These results were highly non-normal count data (Shapiro-Wilkes test, p<0.0001), so Poisson regression was used to determine the relationship between the number of deer pellet groups collected in a subplot and its distance to the woodlot edge.
Results

Browse Preference

Out of the established 45 pairs of *L. maackii* shrubs, 42 retained their flagging through the end of the study. I observed new deer browse on 40 of these pairs (95%, Figure 3). Most of these pairs (55%) had more new deer browse on the fruiting branches, but some (31%) had more new deer browse incidence on branches with fruits removed. Only 9% of pairs had the same amount of new deer browse on both treatments. A sign test indicated that there was no significant difference in probability that a deer will browse more heavily on either treatment (fruits intact vs. fruits removed, p>0.05).

Seed Shadow Projection

Combining deer gut retention time data and sex-specific daily movement data, I projected distinct seed shadows for *L. maackii* seed dispersal by male and female deer. These seed shadows project a peak in *L. maackii* seed dispersal at 300m by female deer and at 900m by male deer (Figure 4). Dispersal kernels were fit to these projections, providing a continuous function to describe these patterns (Figure 5). AIC indicated that the female seed shadow projection fit a lognormal distribution much better than a normal or negative exponential distribution, whereas the male seed shadow projection fit a normal distribution best (Appendix 7). While peak frequencies for in dispersal distances were less than 1km for both male and female deer, long-distance dispersal events were also projected for both sexes (Table 1). Male deer were projected to disperse seeds over long distances more frequently than female deer. Male deer dispersed 43.9% of seeds over 1km, whereas female deer dispersed only 7.1% of seeds over 1km. The bootstrapped one-tailed p-value (p<0.0001) indicates that this difference is significant (Figure 6).

Seed Shadow Observation

I collected 29 deer pellet groups from the invaded site in December and January 2012. *Lonicera maackii* seedlings emerged from 9 pellet groups (31%). The following year, I collected a total of 53 deer pellet groups from the invasion front site between October and December 2013, but no *L. maackii* seedlings emerged from these.

I used patterns in the collection of deer pellet groups found in our subplots as an indication of deer activity in our study area, at both the woodlot and subplot scale. Stepwise linear regression using AIC indicated that at the woodlot scale, the best model of deer pellet deposition only incorporated the distance from each woodlot to the nearest road, although this positive relationship was not significant (p>0.05, Table 2). At the subplot scale, the number of deer pellet groups deposited had a significant negative relationship with distance of each subplot from the woodlot edge, although this did not explain much of the variation in deer pellet group deposition (p=0.01, pseudo-$R^2$=0.03 Figure 8). However, a model with terms added for woodlot identity, and the interaction between woodlot identity and distance to woodlot edge, was significant and substantially improved the model fit (chi-squared test, p>0.001, pseudo-$R^2$=0.34). A similar analysis was planned to determine which predictor variables best explained patterns of *L. maackii* seed dispersal, but no *L. maackii* seedlings emerged from these pellet groups.
**Discussion**

To my knowledge, this is the first comprehensive study to describe how deer disperse *L. maackii* seeds. I investigated the interaction between deer and *L. maackii* seeds at multiple plant life cycle stages, from seeds within fruit to seedling viability after dispersal. Using a combination of experimental, analytical, and observational techniques, I demonstrated that deer are important long-distance seed dispersers of *L. maackii*.

**Deer browse preference**

I found evidence of deer consuming *L. maackii* branches while fruits are ripe, providing an opportunity for seed ingestion and subsequent seed dispersal. Deer browse on *L. maackii* was common throughout the invaded study area in the late fall and winter, with new browse marks observed on almost every shrub pair in our study. Interestingly, my data shows that deer commonly consume vegetative *L. maackii* tissue, but previous studies show that leaves of this shrub are generally not consumed by generalist or specialist arthropod herbivores in North America (Cipollini et al. 2008; Lieurance and Cipollini 2012). This suggests that deer and possibly other mammalian herbivores are the primary consumers of *L. maackii* foliar tissue in its introduced range. Most importantly for dispersal, when deer consume fruiting *L. maackii* branches they ingest seeds along with vegetative tissue. However, the proportion of these seeds that survive deer digestion remains unknown.

Frequent browse on *L. maackii* during the late fall and early winter may be explained by *L. maackii* phenology. Since this invasive shrub is frost tolerant and retains its foliage into early winter when other deciduous woody species have already undergone leaf senescence (McEwan et al. 2009; Wilfong et al. 2009; Johnston et al. 2012), it may be an attractive food source for deer at this time. However, deer are not the sole agents of *L. maackii* fruit removal in the late fall and early winter. During this time, *L. maackii* fruits are also removed by frugivorous birds and abscise due to weather (Bartuszevige et al. 2006b). Future observational studies could determine the proportion of *L. maackii* seeds that survive ingestion by deer, complementing knowledge of passed *L. maackii* seed viability for several bird species (Bartuszevige and Gorchov 2006). When survival of *L. maackii* seeds after deer ingestion is known, it will be possible to determine the relative importance of deer and frugivorous birds on *L. maackii* seed dispersal.

Dichromatic color vision in 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 such as bright red colors (Schaefer et al. 2006). At least 12 species of birds in southwestern Ohio consume *L. maackii* berries, which are bright red (Ingold and Craycroft 1983; Bartuszevige and Gorchov 2006b). However, many mammalian herbivores, including 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). This difference in photosensitivity between birds and mammalian herbivores likely explains why fruits of so many temperate plant species evolved bright red colors, since attraction of herbivores to fruit-laden branches could result in increased damage through herbivory (Willson and Whelan 1990). In summary, while deer consume woody tissue of *L. maackii* that bears fruit, these fruits do not attract deer in the same way that fruits attract many avian
frugivores. Consequently, deer may not preferentially consume ripe *L. maackii* fruit, but they do consume them while browsing.

**Seed shadow projection**

This seed shadow projection builds upon the understanding of deer-mediated seed dispersal described in a previous seed shadow projection of *Trillium grandiflorum* (Vellend et al. 2003). Interestingly, the mean dispersal distance for female deer in my projection was 300m, which was also the mean dispersal distance projected by Vellend et al. (2003). My seed shadow projection shows a greater maximum dispersal distance (7.9 km) than this previous projection (3.9 km), and showed that male and female deer are not equally likely to disperse seeds over long distances. Thus, my model suggests that deer in this landscape have a greater long-distance seed dispersal capacity than previously recognized, although Vellend et al.’s (2003) and my maximum dispersal distances are on the same order of magnitude. While these two seed shadow projection showed differences in some key parameters, the hourly movement data used in this analysis, and the analysis of published gut retention time data gives us confidence that these results are representative of *L. maackii* seed dispersal in its introduced range.

The hourly movement data used in this seed shadow projection came from an exceptionally large dataset (Kjaer et al. 2008). While movement data were recorded for 30 deer year-round, I used only the movement data for the months of September through December, because *L. maackii* fruits ripen in September and are mostly gone by the end of December (Bartuszevige et al. 2006b). Movement data used in this study were also collected hourly, eliminating the need to extrapolate between position readings taken several hours apart, as done in Vellend et al. (2003). The southern Illinois landscape where movement data were collected was similar to the western Ohio invasion front, as both consisted of woodlots in an agricultural matrix. Although the southern Illinois landscape had more forest cover (57% of study area) than the Ohio invasion front (18%), the high degree of woodlot isolation in both study areas gives me confidence that deer movement would be similar, as opposed to study areas with more contiguous forests. These considerations were not made in Vellend et al. (2003), which compiled movement data from five US states at various times of year. Therefore, the movement data used in this study were appropriate for projecting patterns of seed dispersal in a fragmented agricultural matrix where *L. maackii* is invading.

A more trivial difference between these seed shadow projections was my use of a lognormal distribution to model retention time, as opposed to the use of a gamma distribution by Vellend et al. (2003). Pond et al. (1988) suggested modeling ruminant gut passage time with a gamma distribution, which more realistically described the first appearance time in these animals compared to the previously popular exponential distribution. However, key features of these gut retention time data (such as first appearance time, mean retention time, and maximum retention time) are nearly identical between lognormal and gamma distributions (Rawesthorne et al. 2006), indicating that the choice between these distributions does not greatly affect the resulting seed shadow projection.

One drawback of my approach was the use of gut retention time data collected from feeding trials of a single captive male adult deer (Mautz and Petrides 1971) for all seed shadow projections. Vellend et al. (2003)’s seed shadow projection relied on feeding trials for six captive deer, both male and female adults, fed guajillo, a common rangeland plant (Barnes et al. 1992). However, I felt that
the sumac inflorescence diet employed by Mautz and Petrides (1971) better reflected the diet available in late fall and early winter for deer in my study areas. Moreover, deer have highly plastic digestive systems which shorten in autumn and lengthen in summer in response to changes in food availability (Weckerly 1989). This means that the distribution of retention times for a single food source could vary within a single deer, depending on the time of year which the data were collected. Mautz and Petrides (1971) do not mention what time of year their data were collected, introducing a possible source of error into this seed shadow projection.

Additionally, the effect of environmental factors on deer retention time are poorly understood. A review by Warner (1981) found that in several species of mammals, retention time is inversely correlated with both temperature and activity level. The gut retention time distributions reported by Mautz and Petrides (1971) were collected from inactive deer kept in relatively small pens. Therefore, these retention times are likely longer than those of deer moving around the invasion front, and this analysis may overestimate dispersal distances produced by deer. On the other hand, if these pens were significantly warmer than conditions experienced by unsheltered deer on the invasion front, these retention times would be faster than those retention times in unpenned deer, meaning that this analysis may underestimate dispersal distances. Determining gut retention time distributions of deer on the invasion front would improve projections of invasive plant seed dispersal by deer.

It is well understood that male deer typically have larger home ranges than female deer, especially during rut in the late fall (Nixon et al. 1971, Walter et al. 2009), however this is the first study to suggest that differences in movement between male and female deer result in different seed shadows. Retention time distributions should also differ between male and female deer. Retention time varies allometrically in mammalian herbivores, with larger animals having longer mean and maximum retention times (Demment and Van Soest 1985). Almost always, male deer are larger than female deer at maturity. Therefore, including sex-specific retention time distributions in seed shadow projections would magnify the greater contribution of male deer to long-distance seed dispersal of invasive plants.

The important parameters of mean and maximum dispersal distance varies among dispersal vector taxa, but appears to depend on the body size of the dispersal vector. The mean projected and observed dispersal distance for many bird species is <100m, and maximum dispersal distances are only on the order of hundreds of meters (Murray 1988; Carlo et al. 2013). Both parameters represent a significantly shorter distance than those projected for deer here and in Vellend et al. (2003). Studies of seed dispersal in large-bodied omnivores are rare, but the Asiatic black bear (Ursus thibetanus) has a projected seed shadow with mean distances ranging from 250m to 1000m, and maximum dispersal distances up to 22,000 meters (Koike et al. 2011), which is about triple the maximum dispersal distance of deer. Together, these studies point to a simple pattern: larger animal dispersal vectors have longer mean and maximum dispersal distances. In the Midwest US, where L. maackii and various other invasive shrubs are invading, deer are almost always the largest mammalian seed dispersal vectors present, especially in fragmented agricultural landscapes. This suggests that deer are responsible for the longest dispersal events for L. maackii in these landscapes. However, the distribution of distances over which a vector dispersers seeds provides only one axis on which it is possible to evaluate the importance of deer in the seed dispersal of invasive plants. As previously
discussed, this study does not quantify the number of seeds consumed by deer that survive digestion, which also contributes to this species’ importance as a dispersal vector.

**Observed Seed Shadow**

Given that the seed shadows in this study projected 43% of dispersal events by female deer and 92% of dispersal events by male deer to take place between 500m – 2100m from a seed source, I expected to find evidence supporting this pattern in the invaded study area where woodlots ranged from approximately 500m to approximately 2100m from the closest seed source. Despite collecting 53 deer pellet groups which had germinable seeds from 13 identified species (Guiden, unpublished data), no germinable *L. maackii* seeds were found. This was not wholly unexpected, given the low abundance of fruiting *L. maackii* along the invasion front. However, I collected 29 pellet groups from the invaded study area, and 31% contained germinable *L. maackii* seeds. This frequency is similar to deer dispersal of an invasive congeneric hybrid (*Lonicera* aff. *X bella*) in central New York, where 11% of collected pellet groups contained germinable seeds (Myers et al. 2004). The presence of germinable *Lonicera* seeds in deer pellets across this genus’ introduced range reinforces the idea that deer disperse invasive *L. maackii* seeds. However it seems that seed dispersal by deer is uncommon along an invasion front.

The difference in deer-mediated *L. maackii* seed dispersal between the invaded area and the invasion front could be explained by several factors. First, some deer pellet groups collected in the invasion front showed evidence of seed predation. Since I collected deer pellet groups every two weeks, seeds within these pellet groups were vulnerable to predation by rodents or arthropods between collections. Therefore, it is possible that *L. maackii* were actually dispersed by deer in this landscape, but faced high mortality from seed predation and hence did not emerge from deer pellets in the greenhouse. However, this explanation is unlikely, since rodent seed predators avoid invasive *Lonicera morrowii* seeds in favor of native seeds (White et al. 1992; Rose et al. 2014).

Another explanation for the observed discrepancies in seed dispersal patterns between sites invokes optimal foraging theory. 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. Fecund *L. maackii* shrubs were by definition rare in the invasion front study area, while *L. maackii* is one of the most common plant species in the invaded study area (Pfeiffer and Gorchov, in press). Where it establishes, *L. maackii* is associated with declines in forest herb, seedling, and sapling layers (Hartman and McCarthy 2008), which constitute important elements of deer diets (Vangilder et al. 1982; Johnson et al. 1995). As the abundance of preferred food sources declines, large herbivores should forage more on less preferred plant species (van Beest et al. 2010). If *L. maackii* continues to spread within the invasion frontier landscape, causing declines in native plant species that deer prefer, I would expect increased *L. maackii* consumption and seed dispersal.

Alternatively, differences in deer abundance may drive these patterns. While my data estimated deer density along the invasion frontier to be 1.2 deer km$^{-2}$ (Appendix 1), studies conducted in the invaded site estimated deer density to be 6.7 deer km$^{-2}$ at the same time of year. Higher deer density can alter foraging behavior, resulting in the inclusion of more low-quality browse. Evidence for this comes from Horsley et al.’s (2003) manipulation of deer densities with enclosures, as opposed to traditional deer exclosure experiments. They found that mean cover of
preferred plant species (*Acer saccharum* and *Rubus*) was slightly lower after 10 years of intermediate and high deer density treatments (8, 15, and 25 deer km\(^{-2}\)) compared to low deer density treatments (4 deer km\(^{-2}\)). However, the mean cover of non-preferred plant species (*Prunus*) followed a negative quadratic trend, and was lowest at the highest deer density treatment (25 deer km\(^{-2}\)). A similar process may explain differences in seed dispersal of invasive *L. maackii* shrubs: once a deer density threshold is reached, consumption of *L. maackii* by deer increases, presumably including viable *L. maackii* seeds. However, at present the relative importance of invasive plant abundance and deer abundance in promoting seed dispersal remains unknown.

Together, these results show that long-distance dispersal of *L. maackii* seeds by deer is less important for spreading *L. maackii* to new areas than I originally hypothesized. However, long-distance seed dispersal presumably occurs in areas with high *L. maackii* abundance, with potential importance for population dynamics and genetic structure. For example, seed dispersal provides an avenue for the introduction of new genetic material to an existing population, enhancing its genetic diversity (Excoffier et al. 2009). *Lonicerma maackii* populations in south-western Ohio already exhibit high levels of diversity that suggest frequent long-distance seed dispersal among populations of this invasive shrub (Barriball et al. in review). Additionally, long-distance seed dispersal of invasive *L. maackii* seeds through deer can rescue populations of this invasive shrub 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). Seeds that are dispersed over long-distances may also face lower intra-specific seedling competition, leading to lower rates of seedling mortality and increased rates of establishment (Janzen 1970). Long-distance seed dispersal by deer, therefore, represents a mechanism through which invasive plants can continue to survive and persist, despite eradication efforts.

This analysis provides some concrete implications for management of *L. maackii*, and possibly other invasive plant species dispersed by deer. My seed shadow projection indicates that bucks are more important in long-distance seed dispersal of *L. maackii*, and likely other invasive plant species, due to longer movements of male deer during rut. Therefore, keeping the abundance of bucks low may slow the spread of *L. maackii* and other invasive plants dispersed by deer. However, I recognize that my model projections could be refined by an increased understanding of gut retention time differences between male and female deer in natural areas.

While reports of exotic species seed dispersal by deer are becoming increasingly common in the literature (Vellend 2002; Myers et al. 2004; Williams & Ward 2006), my research highlights the complex interactions between deer and plant communities. In this research, I demonstrate that deer-mediated seed dispersal can differ according to both intrinsic factors, such as deer sex, and extrinsic factors, such as deer and/or plant abundances. Since North American deer abundances have increased dramatically since pre-colonial times (McCabe and McCabe 1997), understanding how seed dispersal by 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. We should shift efforts beyond compiling lists of plant species that are dispersed by deer into more dynamic research that teases apart the factors that effect this process. By doing so, we will gain a more holistic understanding of how deer facilitate the success of invasive species, in addition to selective herbivory.


Table 1: Percent of dispersal events predicted to occur over long distances (>1km) by the projected seed shadow, broken down by sex.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Does</th>
<th>Bucks</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt;1000m</td>
<td>7.1</td>
<td>43.9</td>
</tr>
<tr>
<td>&gt;2000m</td>
<td>2.0</td>
<td>1.5</td>
</tr>
<tr>
<td>&gt;3000m</td>
<td>1.0</td>
<td>0</td>
</tr>
<tr>
<td>&gt;4000m</td>
<td>0.1</td>
<td>0</td>
</tr>
<tr>
<td>&gt;5000m</td>
<td>0.1</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 2: Stepwise linear regression results for a model describing the total number of deer pellet groups collected at the woodlot scale, based on AIC. Final model was not a significant predictor of the number of deer pellet groups collected (p>0.05).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Deer Pellets=1.8</td>
<td>26.3</td>
</tr>
<tr>
<td>Number of Deer Pellets=0.01 x Distance to Road+1.8</td>
<td>25.9</td>
</tr>
</tbody>
</table>
Figure 1: Invasion front study site (Darke County, Ohio) where deer pellet groups were collected along transects. Known *L. maackii* seed sources are marked as red stars. Woodlots where deer pellet groups were collected were free of reproducing *L. maackii*. Inset shows a magnified woodlot with subplots, each 20m², represented as blue points.
Figure 2: Differentiation between twig browse and branch browse in the browse preference study. The branch on the left experiences twig browse, where only the new terminal growth has been consumed. The branch on the right experiences branch browse, where multiple twigs are consumed along with the woody tissue supporting them. For the sign test, I gave preference to branch browse.
Figure 3: White-tailed deer preference among paired *L. maackii* shrubs assigned to fruit removal treatments and control treatments (fruits left intact). Twenty-three shrub pairs showed greater increases in deer browse on the shrub with fruits left intact, while 13 showed greater increases in deer browse on shrubs with fruits removed. A sign test indicates that this difference is not significant. Four shrub pairs showed equal increase in deer browse between treatments, and two shrub pairs showed no change in deer browse.
Figure 4: Projected seed shadows for dispersal of *L. maackii* seeds by male (blue) and female (red) deer. Error bars represent 95% confidence intervals. Bars represent the probability that a *L. maackii* seed will be dispersed to each 100m distance class. Females were most likely to disperse seeds 300m away from the seed source, while males were most likely to disperse seeds 900m away from the seed source.
Figure 5: Dispersal kernels for projected male and female dispersal of *L. maackii* seeds. The female kernel was defined by a log-scale parameter of 1.40 and a shape parameter of 0.74. The male kernel was defined by a mean of 9.87 and a standard deviation of 3.81. Differences in dispersal kernels arose from significantly different seed shadow projections to which they were fit (Fig. 4).
Figure 6: Histogram depicting the proportion of seeds dispersed more than 1km from a *L. maackii* seed source in 10,000 projected seed shadows for female deer dispersal of *L. maackii* seeds. The dashed line represents the proportion of seeds dispersed more than 1km in a projected seed shadow for male deer dispersal of *L. maackii* seeds. No projected seed shadows using female deer movement data had a higher proportion of seeds dispersed over 1km than the projected seed shadow using male movement data, (p>0.00001).
Figure 7: Relationship between the number of collected deer pellet groups in each subplot and the distance from woodlot edge, based on a Poisson-distribution generalized linear model (p=0.01).
Appendices

Appendix 1: Estimating Deer Population Density

The abundance of fresh pellet groups was used to develop a rough idea of deer abundance in the invasion front study area. This index is simple to implement, and is represented by the following equation (adapted from Eberhardt and van Etten 1956):

\[
\text{Deer km}^{-2} = \frac{\text{(Number of Pellet Groups)}}{\text{(Pellet Groups Depo}sted \times \text{Deer}^{-1} \times \text{Day}^{-1}) \times \text{Number of Days} \times \text{Area Surveyed}}
\]

Over an 84-day collection period, I collected 53 pellet groups. The subplots represent a total area of 0.039 km\(^2\), and 12.7 pellets per deer per day is a commonly employed value for the defecation rate parameter in the winter (Eberhardt and van Etten 1956). With these values, I estimated that late fall and early winter deer abundance in the invasion front was 1.2 deer km\(^{-2}\). However, I recognize two possible sources of error in this deer density estimate. The first is the shortening of the deer digestive tract during the transition between summer and winter (Weckerly 1989). Without an understanding of the variability of defecation rate, this analysis may over- or underestimate deer density. Additionally, leaf fall may cover recently deposited deer pellets, hence violating one of the assumptions of this index.

To understand how the latter may have affected my ability to find deer pellet groups, I recorded the change in visibility of 10cm PVC pipe markers leaf litter depth in each woodlot where deer pellets were collected (Figure A.1). At the beginning of this study 100% of these markers were visible, with little change through the end of October, since this was prior to leaf senescence. However, at beginning of November we saw larger decreases in marker visibility, with the largest decrease in visibility occurring between October 29\(^{th}\) and November 14\(^{th}\), as a pulse of leaf fall occurred with the onset of cold weather. Not surprisingly, I found the fewest deer pellet groups during this time, suggesting that my collection methods were sensitive to forest floor visibility. Little change in marker visibility occurred between November and December, since most deciduous leaves had already fallen.
Figure A.1: Percent visibility time series describing the change in forest floor visibility throughout the duration of deer pellet collection, between October and December 2013.
Appendix 2: Detailed Description of Fine Scale Movement Data

I obtained hourly deer movement data from a study originally investigating doe home range overlaps (Kjaer et al. 2008), from collaborators Eric Schauber and Clay Nielsen. This dataset consisted of 39,697 hourly readings of deer position using GPS collars, over a five-year period (2002-2006) in southern Illinois. However, not all deer had the same amount of position data collected from them, since these deer were sedated and collared at various times and years (Figure A.2). These movement data were organized into approximately 550 72-hour movement periods for this seed shadow projection. Due to the small amount of male movement data available, only 3 male 72-hour movement periods, all obtained from the same male, were available for analysis. Due to the uneven amount of data collected for deer, the number of 72-hour movement periods contributed by each female deer ranged from 7 (Deer ID# 15) to 56 (Deer ID#1). Movement data for some deer were excluded from our analysis since they were not followed during the late fall and early winter (Deer ID #’s 6-9).

Figure A.2: Histogram describing the amount of hourly position data collected for each of the 26 deer in the dataset obtained from Kjaer et al. (2008). Note the small amount of data obtained from the sole male deer, Deer #5.
Appendix 3: Seed Shadow Projection by Age

In addition to the overall seed shadow projection and separate seed shadow projections for male and female deer, I also projected a seed shadow for the three age classes of deer in our dataset (fawn, yearling, adult). Adults were most represented in this dataset with 433 72-hour movement periods, followed by yearlings with 291 72-hour movement periods, and fawns with 31 72-hour movement periods. If the three age classes each had a unique seed shadow projection, it would be appropriate to include interactions between age class and sex in our analyses. However, peak widths and peak heights were similar among projected seed shadows for each age class (Figure A.3). This justifies pooling all female deer for analysis.

Figure A.3: Seed shadow projections for female deer, broken down by age class (adult, yearling, fawn) based on unique fine scale movement data for each age class.
Appendix 4: R Code for Seed Shadow Projections

###Load required packages (install first)
library(ggplot2)
library(MASS)

+++++++++++++++++++++++Retention Time+++++++++++++++++++++++  
###Import data estimates from Mautz&Petrides 1971
RET=c(rep(7.5,1),rep(12.5,3),rep(17.5,7),rep(22.25,12),  
      rep(27.5,36),rep(32.5,10),rep(37.5,11),rep(42.5,9),  
      rep(47.5,5),rep(52.5,4),rep(57.5,1),rep(62.5,1))
#Check distributions
hist(RET,freq=T,xlim=c(1,72),breaks=c(seq(0,80,5)),ylim=c(0,40))
#Define lognormal parameters
sigma=sqrt(log(1+(sd(RET)/mean(RET))^2))
mu=log(mean(RET))-0.5*(sigma^2)
#What time scale should we use? (At what hour are 99% of seeds passed)
qlnorm(0.99,meanlog=mu,sdlog=sigma)
#Plot retention times over 72 hours
LogNorm=function(mean,SD,times){
  sigma=sqrt(log(1+(SD/mean)^2))
  mu=log(mean)-0.5*(sigma^2)
  RetMatrix=matrix((dlnorm(times,meanlog=mu,sdlog=sigma)),ncol=1)
  plot(as.vector(RetMatrix))
  return(RetMatrix)
}
Ret.Mat=LogNorm(mean(RET),sd(RET),1:72)
Ret.Mat=as.vector(Ret.Mat)

+++++++++++++++++++++++HOURLY MOVEMENT+++++++++++++++++++++++  
#Read data file
Data=read.csv("Deer displacement.csv")
#Define starting location for each 72-hour period (1800 hours)
Start.X=Data$X[seq(1,(length(Data$X-72)),72)]
Start.Y=Data$Y[seq(1,(length(Data$Y-72)),72)]
#Establish formula for displacement, UTM coordinate system is in meters
Displacement=function(x1,x2,y1,y2){
  Disp.Mat=matrix(nrow=length(x2),ncol=5,byrow=F)
  Disp.Rep.X=matrix(nrow=72,ncol=length(x1),byrow=F)
  Disp.Rep.Y=matrix(nrow=72,ncol=length(x1),byrow=F)
  for(i in 1:length(x1)) Disp.Rep.X[,i]=x1[i]
  Disp.Mat[,1]=as.vector(Disp.Rep.X)
  Disp.Mat[,2]=x2
  for(i in 1:length(y1)) Disp.Rep.Y[i]=y1[i]
  Disp.Mat[,4]=y2
  for(i in 1:length(x2)) Disp.Mat[i,5]=
    sqrt((Disp.Mat[i,2]-Disp.Mat[i,1])^2+(Disp.Mat[i,4]-Disp.Mat[i,3])^2)
Disp=as.vector(Disp.Mat[,5])
return(Disp)

#Now run this formula, using start coordinates for each mvmt period
Data$Disp=Displacement(Start.X,Data$X,Start.Y,Data$Y)
#Make sure that first hour equals 0m displacement for each mvmt period
Zero.Check=subset(Data,Data$Disp==0)
#Exclude NA values (these will mess with summary stats)
max(na.exclude(Data$Disp))
hist(na.exclude(Data$Disp))
DATA0=na.exclude(Data)
DISP0=DATA0$Disp
IDO=DATA0$ID

#Generate histogram describing amount of data for each deer in dataset
PLOT=data.frame(ID0,DISP0)
ggplot(PLOT,aes(x=ID)) +
  geom_histogram(color="black",fill="grey50",binwidth=1) +
  xlab("Deer ID Number") +
  ylab("Frequency") +
  scale_x_continuous(breaks=seq(from=0,to=30,by=5)) +
  theme_bw() +
  theme(axis.title.x=element_text(face="bold",family="serif",size=18,vjust=-0.5)) +
  theme(axis.title.y=element_text(face="bold",family="serif",size=18)) +
  theme(axis.text.x=element_text(size=16,family="serif",angle=0,vjust=-0.005)) +
  theme(axis.text.y=element_text(size=16,family="serif"))

##Examine the factors affecting movement: age, sex, date
All.Mat=matrix(Data$Disp,nrow=72)
All.Disp=apply(All.Mat,1,mean,na.rm=T)
Time=1:72

#sex
Males=subset(Data,Data$Sex=="Mal")
Male.Mat=matrix(Males$Disp,nrow=72)
Male.Disp=apply(Male.Mat,1,mean,na.rm=T)
Females=subset(Data,Data$Sex=="Fem")
Female.Mat=matrix(Females$Disp,nrow=72)
Female.Disp=apply(Female.Mat,1,mean,na.rm=T)
plot(Male.Disp~Time,
col="red",type="l",
xlab="Time (Hours)",ylab="Displacement")
points(Female.Disp,col="blue",type="l")
legend(x=1450,legend=c("Male","Female"),
col=c("red","blue"),ty=c(1,1),cex=0.65)

#age
Fawns=subset(Data,Data$Age=="F")
Fawns.Mat=matrix(Fawns$Disp,nrow=72)
Fawns.Disp=apply(Fawns.Mat,1,mean,na.rm=T)
Yearlings=subset(Data,Data$Age=="Y")
Yearlings=subset(Yearlings,Yearlings$Sex=="Fem")
Yearlings.Mat=matrix(Yearlings$Disp,nrow=72)
Yearlings.Disp=apply(Yearlings.Mat,1,mean,na.rm=T)
Adults=subset(Data,Data$Age=="A")
Adults.Mat=matrix(Adults$Disp,nrow=72)
Adults.Disp=apply(Adults.Mat,1,mean,na.rm=T)
plot(Adults.Disp~Time,col="red",type="l",ylim=c(0,700),
  xlab="Time (Hours)",ylab="Displacement")
points(Fawns.Disp,col="blue",type="l")
points(Yearlings.Disp,col="green",type="l")
legend(x=650,legend=c("Adults","Yearlings","Fawns"),
  col=c("red","green","blue"),lty=c(1,1),cex=0.65)

#date
Sep=subset(Data,Data$Month=="Sep")
Sep.Mat=matrix(Sep$Disp,nrow=72)
Sep.Disp=apply(Sep.Mat,1,mean,na.rm=T)
Oct=subset(Data,Data$Month=="Oct")
Oct.Mat=matrix(Oct$Disp,nrow=72)
Oct.Disp=apply(Oct.Mat,1,mean,na.rm=T)
Nov=subset(Data,Data$Month=="Nov")
Nov.Mat=matrix(Nov$Disp,nrow=72)
Nov.Disp=apply(Nov.Mat,1,mean,na.rm=T)
Dec=subset(Data,Data$Month=="Dec")
Dec.Mat=matrix(Dec$Disp,nrow=72)
Dec.Disp=apply(Dec.Mat,1,mean,na.rm=T)
plot(Sep.Disp~Time,col="red",type="l",ylim=c(000,800),
  xlab="Time (Hours)",ylab="Displacement")
points(Oct.Disp,col="blue",type="l")
points(Nov.Disp,col="green",type="l")
points(Dec.Disp,col="orange",type="l")
legend(x=750,legend=c("Sept","Oct","Nov","Dec"),
  col=c("red","blue","green","orange"),lty=c(1,1),cex=0.65)
###Need function to divide displacements by 100
##This gives bins in 100m's for seed shadow projection (essential!)
Dist.Class=matrix(Data$Disp,nrow=72,byrow=F)/100
Mat.Func=function(x){
  Mat=matrix(nrow=80)
  for(i in 1:80)
    Mat[i,]=length(subset(x,i-1<x & x<i))/length(na.exclude(x))
  return(matrix(Mat))
}
#Now can calculate overall Seed Shadow
Move.Mat=apply(Dist.Class,1,Mat.Func)
colSums(Move.Mat)
Seed.Shadow=Move.Mat%*%Ret.Mat
#Summarize %long-distance seed dispersal events
Summary.Table=data.frame(Distance=c(">1000m",">2000m",">3000m",
  
  
  
  ">4000m",">5000m"),
  Proportion=c(1-sum(Seed.Shadow[1:10]),
  1-sum(Seed.Shadow[1:20]),

35
Summary: Table
### Break up Seed Shadow into different environmental factors

**#Sex**

Male.Class = matrix(Males$Disp, nrow = 72, byrow = F) / 100

Mat.Func = function(x) {
  Mat = matrix(nrow = 23)
  for (i in 1:23) {
    Mat[i,] = length(subset(x, i-1 < x & x < i)) / length(na.exclude(x))
  }
  return(matrix(Mat))
}

Male.Mat = apply(Male.Class, 1, Mat.Func)
Male.Mat[,45] = 0
Male.Shad = Male.Mat %*% Ret.Mat

Female.Class = matrix(Females$Disp, nrow = 72, byrow = F) / 100

Mat.Func = function(x) {
  Mat = matrix(nrow = 80)
  for (i in 1:80) {
    Mat[i,] = length(subset(x, i-1 < x & x < i)) / length(na.exclude(x))
  }
  return(matrix(Mat))
}

Female.Mat = apply(Female.Class, 1, Mat.Func)
Female.Shad = Female.Mat %*% Ret.Mat

plot(Female.Shad)
points(Male.Shad, col = "red")

**#Age**

Fawn.Class = matrix(Fawns$Disp, nrow = 72, byrow = F) / 100

Mat.Func = function(x) {
  Mat = matrix(nrow = 80)
  for (i in 1:80) {
    Mat[i,] = length(subset(x, i-1 < x & x < i)) / length(na.exclude(x))
  }
  return(matrix(Mat))
}

Fawn.Mat = apply(Fawn.Class, 1, Mat.Func)
Fawn.Shad = Fawn.Mat %*% Ret.Mat

Yearling.Class = matrix(Yearlings$Disp, nrow = 72, byrow = F) / 100

Mat.Func = function(x) {
  Mat = matrix(nrow = 69)
  for (i in 1:69) {
    Mat[i,] = length(subset(x, i-1 < x & x < i)) / length(na.exclude(x))
  }
  return(matrix(Mat))
}

Yearling.Mat = apply(Yearling.Class, 1, Mat.Func)
Year.Shad = Yearling.Mat %*% Ret.Mat
Adult.Class = matrix(Adults$Disp, nrow=72, byrow=F)/100
Mat.Func = function(x) {
  Mat = matrix(nrow=58)
  for(i in 1:58) {
    Mat[i,] = length(subset(x, i-1 < x & x < i))/length(na.exclude(x))
  }
  return(matrix(Mat))
}
Adult.Mat = apply(Adult.Class, 1, Mat.Func)
Adult.Shad = Adult.Mat%*%Ret.Mat

Dist = (1:80)*100
Adult.Shad = c(Adult.Shad, rep(0,22))
Year.Shad = c(Year.Shad, rep(0,11))
PLOT = data.frame(Adult.Shad, Year.Shad, Fawn.Shad, Dist)
ggplot(PLOT, aes(x=Dist, y=Adult.Shad)) +
  geom_line(aes(color="Adults"), size=1.5) +
  geom_line(aes(y=Year.Shad, color="Yearlings"), size=1.5, alpha=4/5) +
  geom_line(aes(y=Fawn.Shad, color="Fawns"), size=1.5, alpha=4/5) +
  scale_colour_manual("",
    breaks=c("Adults", "Yearlings", "Fawns"),
    values=c("firebrick3", "forestgreen", "dodgerblue3")) +
  theme_bw() + theme(panel.grid.major = element_blank()) + ylim(0, 0.20) +
  xlab("Distance from Source (m)") +
  ylab("Proportion of Seeds Dispersed") +
  theme(axis.title.x = element_text(face="bold", family="serif", size=18, vjust=-0.5)) +
  theme(axis.text.x = element_text(size=16, family="serif")) +
  theme(legend.text = element_text(family="serif", size=20)) +
  theme(legend.justification = c(1,1)) +
  theme(legend.position = c(1,1)) +
  theme(legend.text = element_text(family="serif", size=16)) +
  theme(legend.background = element_rect(fill="white", color="black")) +
  guides(fill=guide_legend(title=NULL))

Need to determine what distribution best fits seed shadows for dispersal kernel
Seed.Shadow = as.vector(Seed.Shadow)
Dist = 1:length(Seed.Shadow)*100
Female Seed Shadow
For lognormal, need to replace zeros with small non-zeros
Non.Zeros = subset(Seed.Shadow, Seed.Shadow>0)
Fit.Shadow = ifelse(Seed.Shadow>0, Seed.Shadow, 0.000000000000000001)
#Estimate, similar to retention time distribution
Bin.Shadow = c(rep(1,9), rep(2,14), rep(3,18), rep(4,16), rep(5,12),
  rep(6,9), rep(7,7), rep(8,5), rep(9,3), rep(10,2), rep(11,1),
  rep(13,1), rep(21,1), rep(32,1), rep(60,1))
#Fit each distribution using MASS package, plot each distribution
LN.fit = fitdistr(Bin.Shadow, "lognormal")
AIC(LN.fit)
LN.Kernel = dlnorm(1:80, meanlog = LN.fit$estimate[1], LN.fit$estimate[2])
Norm.fit = fitdistr(Bin.Shadow, "normal")
AIC(Norm.fit)
Norm.Kernel = dnorm(1:80, mean = Norm.fit$estimate[1], sd = Norm.fit$estimate[2])
NE.fit = fitdistr(Bin.Shadow, "exponential")
AIC(NE.fit)
NE.Kernel = dexp(1:80, rate = NE.fit$estimate[1])
PLOT = data.frame(Seed.Shadow, Dist*100, LN.Kernel, NE.Kernel, Norm.Kernel)
ggplot(PLOT, aes(x = Dist*100)) +
  geom_bar(aes(y = Seed.Shadow), stat = "identity", color = "black", fill = "grey50") +
  geom_line(aes(y = LN.Kernel, color = "LogNormal"), size = 1.5) +
  geom_line(aes(y = NE.Kernel, color = "Negative Exponential"), size = 1.5) +
  geom_line(aes(y = Norm.Kernel, color = "Normal"), size = 1.5) +
  theme_bw() +
  theme(panel.grid.major = element_blank()) +
  ylim(c(0, 0.2)) +
  xlab("Distance from Source (m)") +
  ylab("Proportion of Seeds Dispersed") +
  theme(axis.title.x = element_text(face = "bold", family = "serif", size = 18, vjust = -0.5)) +
  theme(axis.title.y = element_text(face = "bold", family = "serif", size = 18)) +
  theme(axis.text.x = element_text(size = 16, family = "serif")) +
  theme(axis.text.y = element_text(size = 16, family = "serif")) +
  scale_colour_manual("",
    breaks = c("LogNormal", "Negative Exponential", "Normal"),
    values = c("firebrick3", "forestgreen", "dodgerblue3")) +
  theme(legend.text = element_text(size = 20)) +
  theme(legend.position = c(1, 1)) +
  theme(legend.justification = c(1, 1)) +
  theme(legend.text = element_text(family = "serif", size = 16)) +
  theme(legend.background = element_rect(fill = "white", color = "black")) +
  guides(fill = guide_legend(title = NULL))

### Male Seed Shadow
Fit.Shadow.M = ifelse(New.Male.Shad > 0, New.Male.Shad, 0.00000000000000000001)
Bin.Shadow.M.M = c(rep(1, 2), rep(3, 5), rep(4, 5), rep(6, 6), rep(7, 5), rep(8, 8),
                   rep(9, 18), rep(10, 10), rep(11, 6), rep(12, 12), rep(13, 5), rep(14, 6),
                   rep(15, 6), rep(16, 2), rep(17, 2), rep(18, 1), rep(20, 1))
LN.fit.M = fitdistr(Bin.Shadow.M, "lognormal")
AIC(LN.fit.M)
LN.Kernel.M = dlnorm(1:80, meanlog = LN.fit.M$estimate[1], LN.fit.M$estimate[2])
Norm.fit.M = fitdistr(Bin.Shadow.M, "normal")
AIC(Norm.fit.M)
NE.fit.M = fitdistr(Bin.Shadow.M, "exponential")
AIC(NE.fit.M)
NE.Kernel.M = dexp(1:80, rate = NE.fit.M$estimate[1])
# Plot
ggplot(PLOT, aes(x = Dist)) +
  geom_bar(aes(y = New.Male.Shad), stat = "identity", color = "black", fill = "grey50") +
  geom_line(aes(y = LN.Kernel.M, color = "LogNormal"), size = 1.5) +
geom_line(aes(y=NE.Kernel.M,color="Negative Exponential"),size=1.5)+
geom_line(aes(y=Norm.Kernel.M,color="Normal"),size=1.5)+
theme_bw()+theme(panel.grid.major=element_blank())+ylim(c(0,0.20))+
xlab("Distance from Source (m)")+
ylab("Proportion of Seeds Dispersed")+
theme(axis.title.x=element_text(face="bold",family="serif",size=18,vjust=-0.5))+
theme(axis.title.y=element_text(face="bold",family="serif",size=18))+
theme(axis.text.x=element_text(size=16,family="serif"))+
theme(axis.text.y=element_text(size=16,family="serif"))+
scale_colour_manual("",
    breaks=c("LogNormal","Negative Exponential","Normal"),
    values=c("firebrick3","forestgreen","dodgerblue3"))+
theme(legend.text=element_text(size=20))+
theme(legend.justification=c(1,1))+
theme(legend.position=c(1,1))+
theme(legend.text=element_text(family="serif",size=16))+
theme(legend.background=element_rect(fill="white",color="black"))+
guides(fill=guide_legend(title=NULL))

#Produce dispersal kernel for each sex
Male.Bin=c(rep(2,2),rep(3,1),rep(4,5),rep(5,4),rep(6,6),rep(7,5),
    rep(8,6),rep(9,18),rep(10,10),rep(11,5),rep(12,12),
    rep(13,7),rep(14,7),rep(15,7),rep(16,2),rep(17,2),rep(20,1))
LN.Male=fitdistr(Male.Bin,"lognormal")
Male.Kernel=dlnorm(1:80,meanlog=LN.Male$estimate[1],sdlog=LN.Male$estimate[2])
Female.Bin=c(rep(1,9),rep(2,14),rep(3,17),rep(4,15),rep(5,12),rep(6,9),rep(7,7),
    rep(8,5),rep(9,3),rep(10,2),rep(11,2),rep(12,1),rep(17,1),rep(19,1),
    rep(32,1),rep(58,1))
LN.Female=fitdistr(Female.Bin,"lognormal")
Female.Kernel=dlnorm(1:80,meanlog=LN.Female$estimate[1],
    sdlog=LN.Female$estimate[2])
plot(Female.Shad)
lines(Female.Kernel)
points(Male.Shad,col="red")
lines(Male.Kernel,col="red")

############################BOOTSTRAP SEED SHADOW PROJECTION VARIANCE#########################

#For some reason, appears that you need dataframe for each deer (very clumsy)
Deer1=subset(Data,Data$ID==1)
Deer2=subset(Data,Data$ID==2)
Deer3=subset(Data,Data$ID==3)
Deer4=subset(Data,Data$ID==4)
Deer10=subset(Data,Data$ID==10)
Deer11=subset(Data,Data$ID==11)
Deer12=subset(Data,Data$ID==12)
Deer13=subset(Data,Data$ID==13)
Deer14=subset(Data,Data$ID==14)
Deer15=subset(Data,Data$ID==15)
Deer16=subset(Data,Data$ID==16)
Deer17 = subset(Data, Data$ID == 17)
Deer18 = subset(Data, Data$ID == 18)
Deer19 = subset(Data, Data$ID == 19)
Deer20 = subset(Data, Data$ID == 20)
Deer21 = subset(Data, Data$ID == 21)
Deer22 = subset(Data, Data$ID == 22)
Deer23 = subset(Data, Data$ID == 23)
Deer24 = subset(Data, Data$ID == 24)
Deer25 = subset(Data, Data$ID == 25)
Deer26 = subset(Data, Data$ID == 26)
Deer27 = subset(Data, Data$ID == 27)
Deer28 = subset(Data, Data$ID == 28)
Deer29 = subset(Data, Data$ID == 29)
Deer30 = subset(Data, Data$ID == 30)

### Now compile into a list (surely there is a better way to do this)
Boot.List = list(Deer1, Deer2, Deer3, Deer4, Deer10, Deer11, Deer12, Deer13, Deer14, Deer15, Deer16, Deer17, Deer18, Deer19, Deer20, Deer21, Deer22, Deer23, Deer24, Deer25, Deer26, Deer27, Deer28, Deer29, Deer30)

## Produce a placeholder
Boot.Shadow = matrix(nrow = 80, ncol = 10000, byrow = T)
Boot.Shadow[,] = 0

## Now perform the actual bootstrap
for (i in 1:10000) {
  Codes = matrix(nrow = 25, ncol = 4, byrow = T)
  Disps = matrix(nrow = 72, ncol = 100, byrow = F)
  for (j in 1:length(Boot.List)) {
    Codes[j,] = sample(as.character(Boot.List[[j]]$Code), size = 4)
    Disps[,j] = (subset(Data$Disp/100, Data$Code == Codes[j,]))
  }
  Codes
  Shadows = apply(Disps, 1, Mat.Func) * Ret.Mat
  matplot(Shadows)
  Boot.Shadow[,i] = Shadows}

## Write results to CSV file to import/export
write.csv(Boot.Shadow, file = "Bootstrap.csv")

## Re-upload results
New.Data = as.matrix(read.csv("Bootstrap.csv", header = F))

## Produce confidence interval dataframe
CI = data.frame(Displacement = (1:80)*100, Prop = rep(NA, 80),
  Upper = rep(NA, 80), Lower = rep(NA, 80), Males = New.Male.Shad)

# Calculate confidence intervals
for (i in 1:80) {
  AAA = New.Data[i,][order(New.Data[i,])]
  CISProp[i] = mean(New.Data[i,])
  CISLower[i] = AAA[250]
  CISUpper[i] = AAA[9750]
}

## Now produce color Plot
limits = aes(ymax = Upper, ymin = Lower)
ggplot(CI, aes(x = Displacement, y = Males, fill = "Males")) +
geom_bar(stat="identity",aes(x=Displacement,y=Prop,fill="Females"),
    color="black")+
geom_bar(stat="identity",color="black",alpha=3/5)+
geom_errorbar(limits,color="black",size=1)+
theme_bw()+theme(panel.grid.major=element_blank())+ylim(c(0,0.23))+
xlab("Distance from Source (m)")+
ylab("Proportion of Seeds Dispersed")+
theme(axis.title.x=element_text(face="bold",family="serif",size=18,vjust=-0.5))+
theme(axis.title.y=element_text(face="bold",family="serif",size=18))+
theme(axis.text.x=element_text(size=16,family="serif"))+
theme(axis.text.y=element_text(size=16,family="serif"))+
theme(plot.title=element_text(size=24))+
scale_fill_manual("",breaks=c("Males","Females"),
    values=c("firebrick3","dodgerblue3"))+
theme(legend.text=element_text(size=20))+
theme(legend.justification=c(1,1))+
theme(legend.position=c(1,1))+
theme(legend.text=element_text(family="serif",size=16))+
theme(legend.background=element_rect(fill="white",color="black"))+
guides(fill=guide_legend(title=NULL))
#Calculate 1-tailed p-value
LongF=New.Data[10:80,]
LongM=matrix(data=(New.Male.Shad)[10:80],nrow=71)
P.Func=function(fem,mal){
    for(i in 1:71)
        DATA=subset(fem[i,],fem[i,]>mal[i,])
    summary=length(DATA)/(71*10000)
    return(summary)}
P.Func(LongF,LongM)
#Graph results
Plot=data.frame(Distance=as.vector(Fem))
ggplot(Plot,aes(x=Distance,y=(..count..)/(sum(..count..))))+
gem_histogram(binwidth=0.01,fill="grey70",color="black")+xlim(0,0.75)+ylim(0,0.16)+
theme_bw()+theme(panel.grid.major=element_blank())+
theme_bw()+theme(panel.grid.major=element_blank())+
ylab("Proportion of Female Seed Shadows")+
theme(plot.title=element_text(size=24))+
gem_vline(xintercept=Long.Male,linetype="longdash")
Appendix 5: Quantifying *Lonicera maackii* Seedlings Dispersed by Deer

In order to quantify the role of deer in dispersal of *L. maackii* seeds, it was necessary to identify viable *L. maackii* seeds contained within collected deer pellet groups. Various methods have been used to describe patterns of deer endozoochory in previous studies, including 1) washing deer pellets and isolating seeds of focal species, followed by seed viability tests in a greenhouse (e.g. Myers et al. 2004, Castellano & Gorchov 2013), and 2) planting intact deer pellets in a greenhouse and recording the identity and abundance of emergent seedlings (e.g. Williams 2006, Guiden 2013).

I conducted a pilot study to determine whether one of these methods was more effective at documenting germinable dispersed *L. maackii* seeds. I opportunistically collected 29 deer pellet groups from the invaded site, 15 in early December and 14 in early January. Collected deer pellet groups were cold stored at 5°C through the end of January. At this time, pellet groups were randomly divided in half, and given each of the two treatments described above. After treatment, pellet groups were planted in a greenhouse maintained at 24°C during the day and 15°C at night, conditions that promote *L. maackii* germination (Hidayati et al. 2000). Seedling emergence was recorded weekly.

Of the 29 pellet groups given the washing treatment, 41% (n=12) contained *L. maackii* seeds. The 29 pellet groups had an average of 3.3 seeds per pellet group and a maximum of 37 seeds. However, not all of these seeds were germinable: only 17% (n=5) of the 29 pellet groups had germinable seeds. It was impossible to quantify the total number of seeds contained within the deer pellets planted intact, but 27% (n=8) of the 29 pellet groups had *L. maackii* seedlings emerge. These similar results indicate that the methods give approximately equivalent information describing the presence of germinable *L. maackii* seeds.

Deer pellets collected in December were more likely to contain *L. maackii* seeds than those collected in January. Combining seed germination data for both the washed pellets and pellets planted intact, I observed *L. maackii* seedling germinating from 40% of pellet groups collected in December, compared to only 28% of pellet groups collected in January. Examining only those pellet groups which were washed prior to planting, more *L. maackii* seeds were found in those pellet groups collected in December (Figure A.4).
Figure A.4: Histogram describing the frequency of various total counts of *L. maackii* seeds found within deer pellet groups collected from the Miami ERC in December 2012 and January 2013. Pellet groups collected in December typically had greater numbers of seeds. These results include counts for only half of each pellet group, since half of each pellet groups was potted intact in a greenhouse.
Appendix 6: Deer Pellet Deposition Patterns

In order to understand patterns of deer activity in our study area, I investigated the relationship of deer pellet deposition at both the woodlot and subplot levels to several variables describing the landscape of each collection area. Deer pellet groups were collected from ten woodlots. Correlation coefficients for the 13 landscape variables investigated are shown below (Table A.1).
Table A.1: Correlation coefficients for 13 landscape variables used as predictors for patterns of deer pellet depositions in ten woodlots. Where correlation between two variables was high (>0.70), the variable with a greater correlation to the number of deer pellets found was retained. An asterisk (*) denotes variables that were retained.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Perimeter</th>
<th>Area</th>
<th>Edge: Area</th>
<th>Distance to Seed Source</th>
<th>Distance to Road</th>
<th>% Woodlot 500m</th>
<th>% Crop 500m</th>
<th>% Residential 500m</th>
<th>% Road 500m</th>
<th>% Wood 1000m</th>
<th>% Crop 1000m</th>
<th>% Residential 1000m</th>
<th>% Road 1000m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perimeter</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Area*</td>
<td>0.984</td>
<td>1</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Edge: Area</td>
<td>-0.913</td>
<td>-0.923</td>
<td>1</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Distance to Seed Source*</td>
<td>0.212</td>
<td>0.301</td>
<td>-0.116</td>
<td>1</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Distance to Road*</td>
<td>0.223</td>
<td>0.173</td>
<td>-0.214</td>
<td>0.244</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Woodlot 500m*</td>
<td>0.266</td>
<td>0.213</td>
<td>-0.133</td>
<td>-0.062</td>
<td>0.078</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Crop 500m</td>
<td>-0.023</td>
<td>0.026</td>
<td>-0.155</td>
<td>0.190</td>
<td>0.103</td>
<td>-0.915</td>
<td>1</td>
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</tr>
<tr>
<td>% Res 500m*</td>
<td>-0.388</td>
<td>-0.455</td>
<td>0.528</td>
<td>-0.393</td>
<td>-0.294</td>
<td>0.437</td>
<td>-0.759</td>
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<tr>
<td>% Road 500m</td>
<td>-0.366</td>
<td>-0.518</td>
<td>0.641</td>
<td>-0.202</td>
<td>-0.637</td>
<td>-0.213</td>
<td>-0.078</td>
<td>0.427</td>
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<td></td>
<td></td>
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<tr>
<td>% Wood 1000m*</td>
<td>-0.302</td>
<td>-0.563</td>
<td>0.456</td>
<td>-0.686</td>
<td>-0.401</td>
<td>0.210</td>
<td>-0.388</td>
<td>0.521</td>
<td>0.317</td>
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<tr>
<td>% Crop 1000m</td>
<td>0.431</td>
<td>0.556</td>
<td>-0.407</td>
<td>0.489</td>
<td>0.799</td>
<td>0.088</td>
<td>-0.143</td>
<td>0.360</td>
<td>-0.618</td>
<td>-0.088</td>
<td>-0.808</td>
<td>1</td>
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<tr>
<td>% Res 1000m</td>
<td>0.089</td>
<td>-0.009</td>
<td>0.077</td>
<td>-0.195</td>
<td>0.455</td>
<td>-0.107</td>
<td>0.023</td>
<td>0.202</td>
<td>-0.336</td>
<td>-0.306</td>
<td>-0.312</td>
<td>1</td>
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<tr>
<td>% Road 1000m</td>
<td>0.337</td>
<td>0.235</td>
<td>-0.234</td>
<td>0.066</td>
<td>0.767</td>
<td>-0.117</td>
<td>0.274</td>
<td>-0.373</td>
<td>-0.517</td>
<td>-0.265</td>
<td>-0.139</td>
<td>0.577</td>
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Appendix 7: Dispersal Kernel Distribution Fitting

In addition to seed shadow projections, it is desirable to fit a continuous dispersal kernel to the distribution of dispersal distances. Three common distribution families used to fit dispersal kernels are normal (Gaussian), negative exponential, and lognormal (Nathan et al. 2012). I fit the seed shadow projections for female deer (Figure A.5) and male deer (Figure A.6) to these three distribution families using the MASS package in R (Venables and Ripley 2002, Figure A.5). AIC indicated that the seed shadow projection for females most appropriately fit a log normal distribution, while the seed shadow projection for males most appropriately fit a normal distribution (Table A.2).

Figure A.5: Seed shadow projection for female deer (gray bars), shown with dispersal kernels fit using normal, negative exponential, and log normal distributions generated with the MASS package in R. The log normal distribution provides the best fit to the projected seed shadow.
Figure A.6: Seed shadow projection for male deer (gray bars), shown with dispersal kernels fit using normal, negative exponential, and log normal distributions generated with the MASS package in R. The normal distribution provides the best fit to the projected seed shadow.

Table A.2: AIC values describing fit of dispersal kernels to seed shadow projection for all deer. The log normal distribution had the lowest AIC, indicating that it was the appropriate choice for this analysis.

<table>
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<tr>
<th>Distribution Family</th>
<th>Female Seed Shadow Projection</th>
<th>Male Seed Shadow Projection</th>
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<tr>
<td>Normal</td>
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<td>Negative Exponential</td>
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<td>Log Normal</td>
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<td>596.1</td>
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