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INVESTIGATING SEED DISPERSAL DISTANCES AND LONG DISTANCE
DISPERSAL MECHANISMS OF THE INVASIVE PLANT,
ALLIARIA PETIOLATA

Christopher A. Loebach

64 Pages

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Alliaria petiolata, an herbaceous biennial plant, has aggressively invaded North American woodlands. It has been extensively studied to understand why it is a successful invader, but certain aspects of its biology have been understudied such as seed dispersal distances and long distance dispersal mechanisms. We experimentally measured *A. petiolata* seed dispersal distances and determined if epizoochory (external animal transport) is a dispersal mechanism. To measure dispersal distances, seed traps were placed around three *A. petiolata* seed point sources to capture dispersed seeds at increasing distances away from the point sources. Eight mathematical functions describing dispersal distances were fitted to seed counts in traps via maximum likelihood. The lognormal and 2Dt functions were selected for analyses and both predicted that seed density rapidly declined as distance increased with mean dispersal distances of 0.56 and 0.52m and 95% of seeds dispersed within 1.22 and 1.14m, respectively.

To determine if epizoochory is a dispersal mechanism, experimental blocks were placed around seven dense *A. petiolata* patches in summers 2013-2014. Each block contained a mammal inclusion treatment (MIT), which increased small mammal activity

over a germination tray filled with potting soil, and a control, which excluded mammal activity. Seeds dispersed into trays were germinated and the seedlings counted. The increased mammal activity in the MIT resulted in significantly more *A. petiolata* seedlings than the control.

Laboratory studies determined if *A. petiolata* seeds can attach and be retained by raccoon (*Procyon lotor*) and white-tailed deer (*Odocoileus virginianus*) fur, common woodland mammals. A small proportion (3-26%) of seeds attached and was retained by raccoon and deer fur. Attachment and retention significantly increased if either the seed or fur was wet (57-98%). These results are the first to experimentally determine that epizoochory is a seed dispersal mechanism of *A. petiolata* with raccoon and deer as likely dispersal agents.

INVESTIGATING SEED DISPERSAL DISTANCES AND LONG DISTANCE
DISPERSAL MECHANISMS OF THE INVASIVE PLANT,
ALLIARIA PETIOLATA

CHRISTOPHER A. LOEBACH

A Thesis Submitted in Partial
Fulfillments of the Requirements
for the Degree of

MASTER OF SCIENCE

School of Biological Sciences

ILLINOIS STATE UNIVERSITY

2015

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ALLIARIA PETIOLATA

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C.A.L.

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CHAPTER I
INVESTIGATING EPIZOOCHORY AS A LONG DISTANCE SEED DISPERSAL
MECHANISM OF THE INVASIVE PLANT *ALLIARIA PETIOLATA*, GARLIC
MUSTARD

Abstract

Long distance seed dispersal is a key driver for invasive plant species spread. Determining dispersal mechanisms is important for understanding how species spread. *Alliaria petiolata* is an invasive plant whose seed dispersal mechanisms are unknown, but epizoochory (external animal transportation) has been suggested. We tested if epizoochory is a method of seed dispersal for *A. petiolata* through a combination of field and laboratory experiments. In the field, experimental blocks were placed around three dense patches of *A. petiolata* in summer of 2013 and around four in 2014. Each block contained a mammal inclusion treatment (MIT), which increased small mammal activity over a germination tray filled with potting soil, and a control, which excluded mammal activity over its tray. Trays were in the field during peak seed dispersal. *A. petiolata* seeds dispersed into trays were germinated were counted. Seedling counts were compared between treatments. Laboratory studies determined if *A. petiolata* seeds can attach and retained by raccoon (*Procyon lotor*) and white-tailed deer (*Odocoileus virginianus*) fur. Field experiment results showed increased mammal activity in the MIT compared to the control, resulting in significantly more *A. petiolata* seedlings in MIT than control trays.

Laboratory studies revealed a small proportion (3-26%) of seeds attached and was retained by raccoon and deer fur with attachment and retention significantly increased if either seed or fur were wet (57-98%). Our results are the first to experimentally determine that epizoochory is a seed dispersal mechanism of *A. petiolata* with raccoon and deer as likely dispersal agents.

Introduction

Determining the mechanisms of long distance dispersal of an invasive plant species is necessary to understand how the species spreads across the landscape. For most plant species, the vast majority of seeds are dispersed within a short distance of the parent plant (Wilson 1993; Kot et al. 1996; Venable et al. 2008) with only a small proportion dispersed long distances (Cain et al. 2000; Nathan 2006; Nathan et al. 2008). However, these relatively rare long distance dispersal events are more important for the spread of a plant species than many short distance dispersal events (Clark et al. 1998; Suarez et al. 2001; Nathan et al. 2003; Theoharides and Dukes 2007; Pergl et al. 2011). Dispersal distances are strongly influenced by the dispersal mechanism (Pakeman 2001; Corlett 2009; Cunze et al. 2013); therefore, determining the dispersal mechanism is crucial for predicting the spread of an invasive plant species.

Epizoochory (external animal transport) is a common long distance seed dispersal mechanism and typically occurs when seeds become attached to and are transported in mammal fur (Hernández and Zaldívar 2013). Plant species adapted for epizoochory typically have fruits/seeds with special adaptations, such as hooks or barbs, which increase the proportion of seeds that attach to and are retained within mammal fur (Cousens et al. 2010; Bullock et al. 2011). However, a lack of adaption for epizoochory

can be offset by high seed production, because even if a low proportion of seeds are dispersed through epizoochory, the amount will increase as seed production increases, regardless of the traits of the seed/fruit (Will and Tackenberg 2008; Couvreur et al. 2008). Therefore, epizoochory can be an important dispersal mechanism for invasive plant species that lack clear adaptations for epizoochory.

Epizoochory can disperse seeds between isolated habitat patches and establish new populations (Couvreur et al. 2004; Freund et al. 2014) or disperse seeds through continuous habitat for range expansion (Will and Tackenberg 2008). The species of the animal disperser strongly influences dispersal distances (Thomson et al. 2010; Guttal et al. 2011). Species that move fast or have large home ranges are more likely to disperse seeds longer distances than slow moving, small home range animals (Cousens et al. 2010). Additionally, the characteristics of a mammal species' fur affects dispersal. Because seeds attach more readily to wooly fur, mammals with wooly fur are more likely to disperse seeds long distances than mammals with straight fur (Will et al. 2007). The behavior of the animal disperser influences where seeds will be dispersed with high amounts of seeds arriving at areas of high animal activity, such as resting sites (Russo et al. 2006). Identifying which animals are dispersal agents vastly improves the accuracy of predictions about the spread of invasive plant species.

Epizoochory has been suggested as a mechanism of long distance dispersal for the invasive herbaceous woodland plant *Alliaria petiolata*, garlic mustard (Brassicaceae: Bieb. [Cavara & Grande]). However, this mechanism has not been experimentally tested and doing so will improve our ability to predict the spread of *A. petiolata* spread and will improve control strategies. If the vast majority of *A. petiolata* seeds are dispersed within

1.22 m (Chapter II) or within two meters of the parent plant as reported in Nuzzo (1999) and Drayton and Primack (1999), then *A. petiolata* populations are predicted to spread at a rate of less than one meter annually, which is below the observed average spread rate of 5.4 m per year (Nuzzo 1999). In addition, *A. petiolata* spreads through the establishment of satellite populations that are well ahead of the invasion front (Nuzzo 1993, 1999; Burls and McClaugherty 2008). Both the rapidly moving invasion front and the establishment of satellite populations indicate the presence of a long distance dispersal mechanism (Nuzzo 1993, 1999; Burls and McClaugherty 2008; Eschtruth and Battles 2011). Cavers et al. (1979) briefly discussed long distance dispersal mechanisms of *A. petiolata* and stated that seeds did not float well but readily adhered to a damp cloth. Therefore, the authors concluded that epizoochory was a likely dispersal mechanism. Blossey (2001) and Evans et al. (2012) also suggested that epizoochory was a likely dispersal mechanism with deer, mice, and other small mammals transporting the seed, but to date, this hypothesis has not been explicitly tested.

The Dispersal Diaspore Database (DDD) (Hintze et al. 2013) contains seed dispersal information for over 2,111 plant species to predict and rank the epizoochory potential of these species by combining two metrics. The first metric was attachment potential, a seed's ability to adhere to fur (Will et al. 2007), and the other metric was retention potential, the ability of the seed to remain adhered once attached (Römermann et al. 2005; Tackenberg et al. 2006). Of the 2,111 species in the index, 64% were better adapted to epizoochory than *A. petiolata*. *Alliaria petiolata* seeds lack any clear adaptations for epizoochory such as hooks or barbs, but they do have several favorable traits including small size and partial exposure in the fruit (Hintze et al. 2013). While these

results are not highly suggestive of epizoochory, they may not have captured *A. petiolata*'s true potential for epizoochory. Many plant species are dispersed long distances by a mechanism for which they have no apparent adaptations (Clark et al. 1998; Higgins and Cain 2003; Myers et al. 2004).

The studies that comprise the DDD found that attachment potential and retention potential differed among the European mammal species tested (Tackenberg et al. 2006; Will et al. 2007). Since epizoochory potential differs among mammal species, it is important to conduct epizoochory tests on mammal species that *A. petiolata* is likely to encounter in North America. The mammals mentioned in Blossey (2001) and Evans et al. (2012) are logical animals to test since it was hypothesized they were vectors involved in *A. petiolata* long distance dispersal. Additionally, the dampness of the fur may also affect epizoochory potential. Tackenberg et al. (2006) found that dampness of the fur did not have a consistent effect on the retention potential for all 19 species they tested, but dampness did increase retention potential for a few species. Cavers et al. (1979) noted that *A. petiolata* seeds readily adhered to a damp cloth suggesting that the seeds may be more likely to stick to damp rather than dry fur.

We hypothesized that epizoochory via North American woodland mammals is a long distance seed dispersal mechanism of *A. petiolata* and tested this hypothesis through field and complimentary laboratory studies. The field study was designed to attract small mammals to experimental areas to determine if high mammal activity caused these areas to accumulate more seeds resulting in higher densities of first-year *A. petiolata* seedlings, than in areas with low mammal activity. Laboratory studies measured attachment potential and retention potential of wet and dry *A. petiolata* seeds applied to wet and dry

fur of raccoon (*Procyon lotor*) and white-tailed deer (*Odocoileus virginianus*) pelts. Our study is the first to demonstrate that epizoochory is a probable long distance seed dispersal mechanism for *A. petiolata*. This information will increase our understanding of how this species is dispersed and improve control strategies.

Methods

Study Species

Alliaria petiolata is native to Eurasia occurring from England to Sweden to Turkestan, northwestern-Himalayas, India and Sri Lanka, and south to Italy and the Mediterranean basin (Tutin et al. 1964; Cavers et al., 1979). The species was first recorded in North America on Long Island, New York in 1868 (Nuzzo 1993, Roberts and Anderson 2001). Since that time, it has spread exponentially and currently occurs in 37 states that stretch from the New England area to the west coast and five Canadian provinces (USDA Plant Database). It is most abundant in northeastern United States and adjacent Canada in deciduous forests (Anderson et al. 1996). *Alliaria petiolata* is a member of the mustard family (Brassicaceae) and is a winter biennial. Germination occurs in late winter or early spring and basal rosettes are formed the first year. During early spring of the second year between the 18 of April and the 13 of May, plants bolt and rapidly increase shoot length with stem elongation of 1.9 cm per day (Anderson et al. 1996). Flowers form in March and April, while fruits develop in May and June. Seeds are dispersed from July to October with peaks occurring in August and September (Anderson et al. 1996). Baskin and Baskin (1992) found that 70% of seeds germinated in the first year under favorable conditions, but seeds can persist in the seed bank up to five years (Baskin and Baskin 1992).

Study Sites

Study sites were located at Parkland's Foundation Merwin Nature Preserve and South Breens Woods. The Merwin Nature Preserve is 25 km and South Breens Woods is 20 km north of Normal, IL USA. The Merwin Nature Preserve is a 325 ha oak-hickory dominated second-growth forest that has been protected from grazing since the 1970's. The South Breens Woods is a four ha oak dominated forest and has been under protection since 1979. *Alliaria petiolata* was present and abundant at both sites.

Epizoochory Field Experiment

To determine if epizoochory occurs in the field, we placed experimental blocks around dense patches of second-year *A. petiolata* plants. In the summer of 2013, blocks were established around the perimeter of three *A. petiolata* patches at the Merwin Nature Preserve. In 2014, blocks were established around one *A. petiolata* patch at Merwin Nature Preserve and at three patches at South Breens Woods. At each *A. petiolata* patch, one block was placed at the perimeter of the patch in each of the four cardinal directions from the patch center for a total of four blocks per patch. In total, there were 28 blocks placed around seven *A. petiolata* patches.

Each block contained a mammal inclusion treatment (MIT) and a control. In both treatments, a germination tray filled with potting soil was placed into the ground so it was flush with the ground surface. The MIT was designed to increase mammal activity over germination trays relative to the control. A control replicate consisted of a wood-frame (11 x 61 x 31 cm) completely covered with 1.2 cm² size wire mesh placed over a germination tray. A MIT replicate consisted of a wooden frame (31 x 61 x 31 cm) covered with 2.5 cm mesh poultry fencing placed over a tray. The two 31 by 31 cm ends

of the MIT were not covered to allow raccoon-sized or smaller mammals to enter. Each frame included a shallow metal pie pan (23 cm diameter) attached to bottom in the center. Only pans in the MIT were filled daily with bait (200 ml equal parts of cracked corn and black oil sunflower seeds) to attract mammals. Within a block, the position of the MIT and control were randomly assigned and were placed one meter apart. All second-year *A. petiolata* plants located within 1.5 m of the block were removed to prevent significant amounts of seed rain from falling into the trays. One motion sensitive camera was placed at each patch to record animal activity around a single block. The MIT and control were both captured within the frame of the camera.

The distance between the blocks placed on the north and south sides of the patch and between the blocks on east and west sides was measured. A sampling line was established between the two blocks that were the furthest apart. Ten equally spaced sampling points were established along the line. At each sampling point, a random whole number was generated between 1 and 100. If the number was odd, a 0.5 m² quadrat was placed that many centimeters to the left of the line or to the right of the line if the number was even. The second-year *A. petiolata* plants within each quadrat were counted to estimate the average density of second-year plants per 1 m².

Trays were placed in the field during peak seed dispersal. In 2013, the trays were in the field from July 3rd to August 7th. In 2014, at South Breens Woods trays were in field from July 2nd to August 8th while at Merwin Nature Preserve trays were out from July 8th to August 8th. After the trays were collected, they were transported to Illinois State University to overwinter outdoors since cold-moist stratification is necessary for seed germination (Baskin and Baskin 1992). The trays were moved to a heated

greenhouse on Feb 20th in 2014 and Feb 16th in 2015. *Alliaria petiolata* seedlings were counted daily until no new seedlings were observed on two consecutive days, because by this time 95% of the trays had no new seedlings for five consecutive days. Counting was terminated on March 22nd and 12th in 2014 and 2015, respectively.

The number of animal visits in the photos recorded by the motion sensitive cameras was counted for each treatment. An animal was considered to have visited the MIT treatment if it entered the frame, while a visit to the control was counted if an animal touched the outside of the frame. The photos were analyzed with a chi-square analysis to determine if there was a significant difference in animal visits between the treatments. The *A. petiolata* seedling counts in the germination trays were analyzed with a mixed linear model (PROC MIXED) to test for a significant difference between the control and MIT. Treatment was a fixed effect while block, block nested within *A. petiolata* patch, and year were included as random effects in the model. The data were square root transformed to meet the assumptions of normality. All statistical tests were performed in SAS[®] software 9.3 (SAS Institute 2012). Alpha levels were set at 0.05 for all tests.

Seed Attachment

The attachment potential of *A. petiolata* seeds was measured using a white-tailed deer and a raccoon pelt. Both of these animals are common within the study sites and across North America. The pelts consisted of the skin of the animal with the fur still attached. The deer fur consisted of 2-3 cm long hairs that were flattened from the front of the animal towards the back. The raccoon fur had 5-6 cm long hairs with many smaller hairs, less than 4 cm, underneath forming a thick undercoat. Both hair types generally stood upright. The pelts were placed between two wood boards with a 25 cm by 25 cm

opening leaving that area of fur uncovered. The two boards were clamped together to secure the pelts. A 9 cm x 16 cm grid of 144, 2 cm x 2 cm squares was centered 15 cm above the fur in a horizontal position with the fur side up. In each trial, 100 *A. petiolata* seeds were dropped singly through randomly selected squares onto the fur. The pelt and frame were then rotated 180 degrees to an upside down position over a collection box and then immediately turned back to the original position. The seeds that fell off and the seeds that remained in or on the fur were removed and counted and the two counts were summed to account for the 100 seeds used in each trial.

To determine if fur moisture affected seed attachment, furs were misted with 40 ml of water using a plastic spray bottle before the seeds were dropped. Since the seeds were difficult to remove from the wet pelts, pelts were dried with a fan after each trial and then the seeds were removed. The moisture of seeds was also manipulated by partially submerging the seeds in water before they were dropped onto the fur. Therefore, the two main effects of this experiment were fur condition and seed condition resulting in four treatment combinations, seed dry and fur dry (SD/FD), seed dry and fur wet (SD/FW), seed wet and fur dry (SW/FD), and seed wet and fur wet (SW/FW). There were 10 replicate trials for the raccoon and deer pelts. Attachment potential was measured as the proportion of seeds that remained attached to the furs after they were rotated. The raccoon and deer pelts were analyzed separately.

To test for a significant effect of seed condition, fur condition and their interaction, the data were aligned and rank transformed (ART) since they could not be transformed to meet assumptions of a parametric Analysis of Variance (ANOVA). Data were aligned by removing the marginal means of all other factors from the response

variable other than the factor for which the alignment was being applied (Wobbrock et al. 2011). For example, to analyze the interaction effect of a two-way factorial, the marginal means of the main effects are removed from each response variable to isolate the interaction effect. The aligned data were then ranked, and a two-way ANOVA (PROC GLM; SAS Institute 2012) was performed on the ranks. Separate ANOVA's were performed for each main effect and the interaction. For a significant interaction, a Tukey post-hoc analysis was performed. The data were aligned and ranked using the ARTool (Wobbrock et al. 2011). The ART is an appropriate alternative to parametric F-tests when analyzing factorial designs (Mansouri et al. 2004). The ART is robust to Type 1 error (Mansouri 1999) and has greater power than parametric F-tests when normality assumptions are not met (Richter and Payton 1999).

Seed Retention

The same deer and raccoon pelts were attached to separate 25 by 38 cm sections of cardboard. Before seeds were attached, the furs were homogenized by combing the furs two times horizontally and vertically using a plastic comb with 4 cm long teeth spaced 0.9 cm apart. A 5 by 10 grid of 2 by 2 cm cells was placed over the furs and two seeds were dropped per cell from a height of two centimeters. Seeds were then combed into the fur with the same method as homogenization. This procedure is similar to previous epizoochory studies (Rommerman et al. 2005; Tackenberg et al. 2006; and Pablos and Peco 2007). The furs were rotated 180 degrees over a collection box to collect the seeds that did not attach. Next the furs were clamped to a collection bin that was attached to a Fisher Vortex Genie 2, which shook the fur and bin horizontally for one hour. The Fisher Vortex abruptly moved the furs back and forth 0.5 cm. The numbers of

horizontal movements were counted for one minute during the first minute, 30th minute, and 59th minute to ensure that each trial had between 145 to 155 movements per minute. To test for the effect of moisture, furs were misted with water with the same process as described in the attachment potential experiment after the seeds were combed into the fur. There were five trials for each fur by moisture combination.

Other studies (Rommerman et al. 2005; Tackenberg et al. 2006; and Pablos and Peco 2007) used a specialized shaking machine that was able to shake furs horizontally and vertically to test for an effect of position on seed retention potential. We were unable to test the effect of fur position since the Fisher Vortex Genie 2 is only capable of moving furs horizontally. However, the results of this study are likely comparable to other studies since fur position was found to have no effect on retention potential (Tackenberg et al. 2006), or only an effect for cattle fur (Pablos and Peco 2007), which was not used in this study.

Retention potential was measured as the proportion of seeds that remained attached after one hour of shaking. For each pelt type, a two-sample t-test (PROC TTEST; SAS Institute 2012) was done to determine if the retention potential was significantly different between wet and dry fur. Unequal variances were assumed and the Satterwaite's test was used as an alternative to the Student's t-test (Ruxton 2006). The mean retention potential was considered significantly greater than zero if the 95% confidence intervals did not overlap with zero.

Results

Field Experiment

The bait that was placed in the MIT was removed daily for the vast majority of pie pans in both years, indicating animals were visiting the treatments. This high level of animal activity at the MIT was supported by the photos from the motion sensitive cameras. For both years and all *A. petiolata* patches combined, the MIT had 951 animal visits which was significantly greater ($\chi^2_{(1,982)}=788.6$, $p<0.0001$) than the 51 visits to the control. The vast majority of animal visits were made by raccoons and it was the only animal recorded at all seven *A. petiolata* patches (Table 1). Raccoons entered the MIT wood frames and stood directly over the germination trays while feeding. Turkeys were the second most common animal visitor, but they were only recorded in the year 2014 and only at the SBW study site. Turkeys and deer were photographed eating the bait, but they were unable to enter the MIT wood frames due to their large body size. Instead, these animals would lie down outside the edge of the frame and stick their head into the open end of the frame to eat the bait. The increased animal activity over the MIT germination trays resulted insignificantly more ($F_{1,27}=129.5$, $p<0.0001$) *A. petiolata* seedlings than control trays. The difference in *A. petiolata* seedling counts between treatments was quite large with the MIT averaging over one order of magnitude more than the control trays (Fig 1).

The seven *A. petiolata* patches used in this experiment varied in patch size and in density of second-year plants (Table 2). While the *A. petiolata* patches differed in size, there appeared to be no pattern to the variation unlike second-year plant density. All patches from summer 2014 had lower second-year plant density than patches from 2013.

However, this difference in density did not affect *A. petiolata* seedling counts in the germination trays. The random variation attributable to *A. petiolata* patch and year to seedling counts were not significant ($p > 0.10$ for each). The variation due to block was estimated to be zero and therefore SAS PROC MIXED did not test for significance.

Seed Attachment

For the deer pelt, the main effect of fur condition ($F_{1,39}=56.44, P<0.0001$), seed condition ($F_{1,39}=110.3, P<0.0001$), and their interaction ($F_{1,39}=59.8, P<0.0001$) significantly affected attachment potential. Fur condition ($F_{1,39}=3920.4, P<0.0001$), seed condition ($F_{1,39}=100.39, P<0.0001$), and their interaction ($F_{1,39}=81.29, P<0.0001$) also significantly affected attachment potential on the raccoon pelt. Seed attachment potential was highest for both pelt types when seeds were wet, regardless of fur condition (Fig. 2a). When seeds were dry, more seeds attached to wet fur than dry fur.

The Tukey follow-up test of the interaction term found significant differences in the ART ranks. For both pelt types, the SD/FW and the SW/FD treatments had significantly higher ranks than the SD/FD and the SW/FW treatments (Fig. 2b). For the SW/FD treatment, the weak effect on attachment potential of the dry fur was overcome by the wet seed resulting in a high attachment potential. For the SD/FW treatment, the weak effect of the dry seed was overcome by the effect of the wet fur resulting again in a high attachment potential. It may seem counterintuitive that the SW/FW had low ART values despite having high attachment potential values, but this is because both wet fur and wet seeds had strong positive effects on attachment potential. However, when these two effects were combined, it did not result in an increase in attachment potential. Therefore, when these main effects were removed from the SW/FW attachment potential

values, the resulting ranks were low. Thus, high attachment potential values will result, if either the seed or fur is wet.

Seed Retention

The retention potential was significantly greater for wet deer fur ($T_{4.63}=29.6$, $p<0.0001$) and wet raccoon fur ($T_{7.27}=74.78$, $p<0.0001$) when compared to dry fur (Fig. 3). The difference in retention potential between wet and dry fur was large for both pelt types. The retention potential for the dry raccoon fur ranged from 2-5% compared to the wet fur which ranged from 94-100%. The retention potential for dry deer fur ranged from 1-6% and it ranged from 81-98% for wet. While the retention potential was significantly lower for dry fur, it was still significantly greater than zero since the 95% confidence intervals did not overlap with zero.

Discussion

This study is the first to provide experimental evidence that epizoochory through woodland animals is a seed dispersal mechanism of *A. petiolata*. The MIT germination trays had significantly more animal visits than the control trays (Table 1) which resulted in the MIT trays having significantly more *A. petiolata* seedlings (Fig. 1). Raccoons are the likely driver of this relationship as they were the most common animal visitor, and they came in the most direct contact with the germination trays compared to turkey and deer. The laboratory studies provide evidence that seeds are capable of dispersing in the fur of mammals because seeds were able to attach and be retained within the raccoon and deer fur (Fig. 2 and 3). However, these results do not rule out the possibility of seeds being dispersed by attachment to hooves, paws, or claws (Gill and Beardall 2001; Heinken et al. 2006; Schulze et al. 2014). In contrast to other studies (Couvreur et al.

2005; Tackenberg et al. 2006), we found attachment potential and retention potential increased if the seeds or fur were wet (Fig. 2 and 3) indicating that environmental conditions are likely to affect *A. petiolata* epizoochory potential. Therefore, *A. petiolata*'s epizoochory potential may increase under wet environmental conditions such as heavy dew or after a rainfall. *Alliaria petiolata* seeds that are retained within deer and raccoon fur have the potential to be dispersed several kilometers as these mammals have large home ranges. The home range size of deer can range from less one km² to more than 10 km² depending on season and age of the deer (Lesage et al. 2000). The home range size of raccoons can range from less than 0.5 km² to more than one km² depending on resource availability and season (Gerht and Fritzel 1998, Beasley et al. 2007)

While *A. petiolata* seeds lack clear adaptations for epizoochory, other studies have also found that seeds without special adaptations for animal dispersal are still capable of epizoochory dispersal, albeit at a lower proportion of total seed production compared to plant species with adaptations (Fisher et al. et al. 1996; Courvreur et al. 2004; Hovstad et al. 2009). A lack of adaptations by *A. petiolata* may be compensated for by high seed production (Anderson et al. 1996; Nuzzo 1999; Susko and Lovett-Doust 2000), because while a low proportion of the total seeds will be dispersed through epizoochory, the actual number dispersed through epizoochory will be numerous (Will and Tackenberg 2008; Couvreur et al. 2008). Additionally, *A. petiolata* may not require a large proportion of seeds to be dispersed long distances to cause range expansion and the establishment of satellite populations as new populations can become established from only a few seeds due to its autogamous breeding system (Anderson et al. 1996).

Therefore, the small proportion of *A. petiolata* seeds that are dispersed long distances through epizoochory is likely sufficient to drive the observed range expansion.

The lack of adaptations for epizoochory by *A. petiolata* may be additionally overcome by the high retention potential of seeds under wet conditions. The retention time of seeds in mammal fur has a stronger effect on dispersal distances than the attachment potential of those seeds. The longer a seed is retained in the fur of an animal, the farther it can be dispersed by that animal (Couvreur et al. 2005; Adriaens et al. 2007; Guttal et al. 2011). Since the retention potential of *A. petiolata* seeds significantly increased when either seeds or fur were wet (Fig. 2 and 3) this retention pattern could result in increased retention time and, therefore, dispersal distances. Epizoochory dispersal is still likely to occur under dry condition since the attachment potential and retention potential were significantly greater than zero when seeds and fur were dry (Fig. 2 and 3), but at a much lower proportion of total seeds produced compared to wet conditions.

The cause for why retention potential, and also attachment potential, increase when the seed or fur are wet is unclear. Some plant species produce seed coat mucilage when wet and this mucilage can have a variety of functions with one being increased epizoochory dispersal (Yang et al. 2012). When *A. petiolata* seeds were observed under a light microscope, they did not appear to produce any mucilage when wet. Another possibility is that the water forms hydrogen bonds between the seeds and fur which increases the retention and attachment potential. However, this idea was not explored in this study and further research is needed to understand the role of water.

Control strategies of *A. petiolata* can be improved by incorporating information about epizoochory seed dispersal. Effective control strategies that prevent the spread of invasive plant species must account for seed dispersal mechanisms (Coutts et al. 2011). One method to prevent spread of *A. petiolata* is to reduce the population size of potential animal dispersal agents, such as deer and raccoons (Constible et al. 2005); however, this method is likely to be infeasible or undesirable for most situations. A different option for preventing spread is to use targeted surveillance for satellite populations in areas with high animal activity as these areas are likely to receive more *A. petiolata* seeds than areas with low animal activity (Heinken et al. 2006; Russo et al. 2006). An example would be to survey deer trails for identification and removal of *A. petiolata* plants since trails have high deer activity and are likely seed dispersal corridors (Lefcort and Pettoello 2012). Another option to prevent the spread would be to target control efforts on *A. petiolata* populations in areas of high animal activity. These populations will contribute more to the spread of *A. petiolata* than isolated populations because they have more seeds being dispersed long distances through epizoochory (Buckley et al. 2005).

Incorporating dispersal distances into control strategies can also be used to isolate *A. petiolata* populations, which may improve control methods. Isolated *A. petiolata* populations experience reduced vigor over time due to the buildup of deleterious alleles through genetic drift (Mullarkey et al. 2013). However, this effect can be reversed by the introduction of genetic material from other populations. The success of control strategies is strongly affected by the vigor of the population with control success increasing as population vigor declines (Evans et al. 2013). Therefore, information about dispersal distances can be used to determine the distance among populations necessary to

dramatically reduce gene flow among the populations, potentially leading to long term reduction of *A. petiolata*. Unfortunately, measuring epizoochory dispersal distances in the field is difficult (Nathan 2006). Several mechanistic models have been developed to predict epizoochory dispersal distances (Russo et al. 2006; Thomson et al. 2010; Will and Tackenberg 2008), but none have been parameterized for the animals from this study. An alternative method would be to base potential dispersal distances on the size of the home ranges of raccoons and deer (Gerht and Fritzel 1998; Lesage et al. 2000).

One surprising result from this study was wild turkeys eating bait from MIT treatments (Table 1). It was assumed that the 31 cm by 31 cm opening of the MIT frame would be small enough to deter larger animals such as turkeys, but this was not the case. Turkeys may have dispersed seeds into the MIT trays in addition to raccoons, but further research is needed to determine if turkeys are seed dispersal agents. For seed dispersal by birds, there have been many studies exploring endozoochory (animal ingestion of seed) (Tewksbury et al. 2002; Clark et al. 2005; Levey et al. 2005), but fewer have explored epizoochory and the majority that have looked at wetland plants attaching to migratory birds (Figuerola and Green 2002). Future research needs to explore if *A. petiolata* seeds and other plant species in general, are able to attach and be retained within the feathers, or any other body part, of turkeys. These large vertebrates may be an unexplored, but important seed dispersal vector.

In conclusion, the results from our study provide strong evidence that epizoochory by deer and raccoon is a seed dispersal mechanism for *A. petiolata*. These results will improve our ability to predict the spread of *A. petiolata* because areas with high animal activity are more likely to have *A. petiolata* seeds deposited there, increasing the risk of

invasion compared to areas with low animal activity. Land managers can incorporate this information into their control strategies by focusing on *A. petiolata* populations in areas with high animal density or traffic and by focusing search areas for new populations in areas with high animal activity. Future research should focus on creating reliable estimates of epizoochory seed dispersal distances.

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Table 1. The photo counts for each animal species that visited the treatments for both study years combined. Turkeys were only observed in 2014. Raccoon was the only animal observed at all seven *A. petiolata* patches.

Animal	MIT	Control
Raccoon	720	46
Turkey	147	0
Deer	32	0
Squirrel	2	2
Nuthatch	9	0
Blue Jay	3	0
Chipmunk	10	2
Mouse	4	0
Cardinal	1	0
Mourning Dove	3	0
Woodchuck	1	0

Table 2. The distance (m) between the north and south blocks and the east and west blocks for each *A. petiolata* patch and the average density of second-year plants per 1m². Patches 1-3 and 4-7 were used in 2013 and 2014, respectively.

Patch	N to S (m)	E to W (m)	Density (m ²)
1	10	16	141
2	9.4	9.4	237
3	22	11.8	258
4	11.3	14.5	41
5	13	11.3	51
6	18.3	13.3	24
7	20	17	60

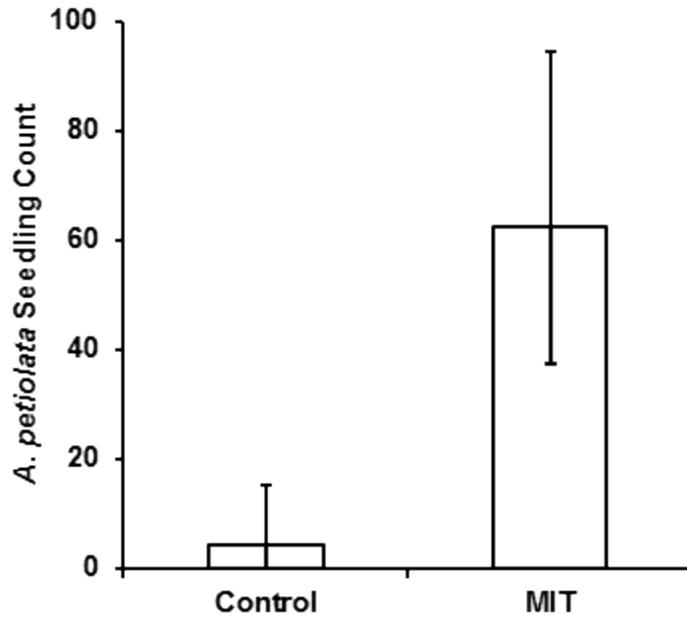


Fig. 1 The back transformed mean number (\pm 95% CI) of *A. petiolata* seedlings counted in the germination trays of the two treatments. The confidence intervals are not symmetrical because of the back transformation. The MIT trays ($p < 0.0001$) had significantly more seedlings than the control trays.

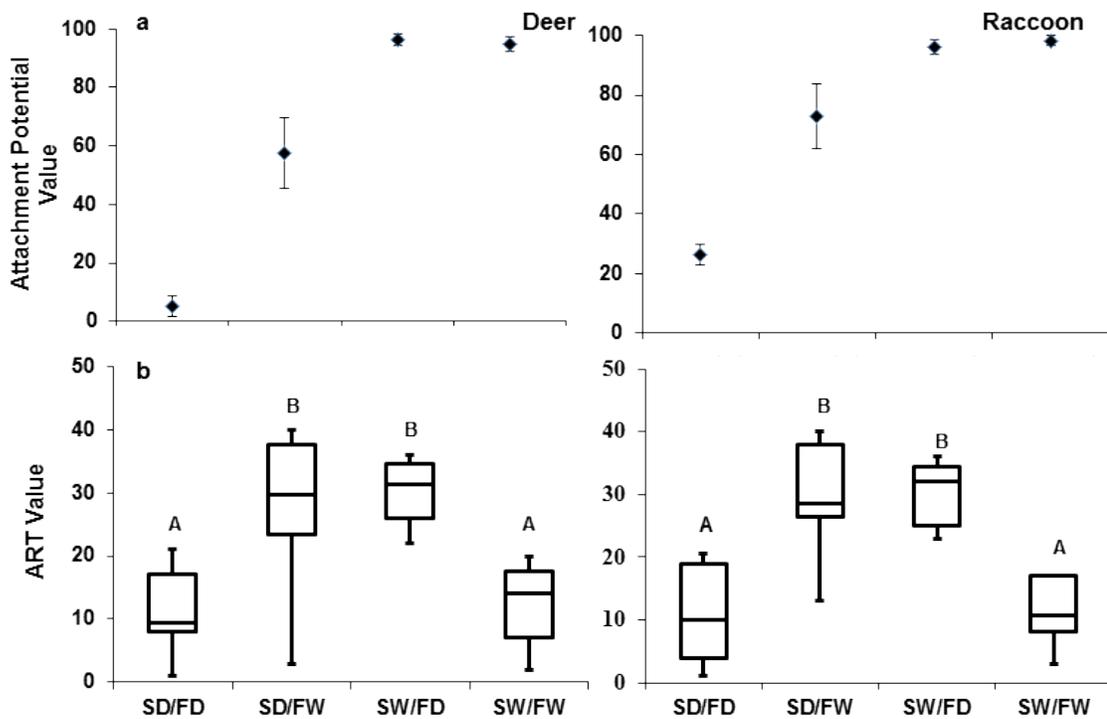


Fig. 2a The mean(\pm standard deviation) attachment potential values for each treatment combination for both the deer and raccoon pelts. **b** The box and whisker plot of results of the Tukey follow test on the ART values of the interaction between seed and fur condition. Significant differences are marked by different letters.

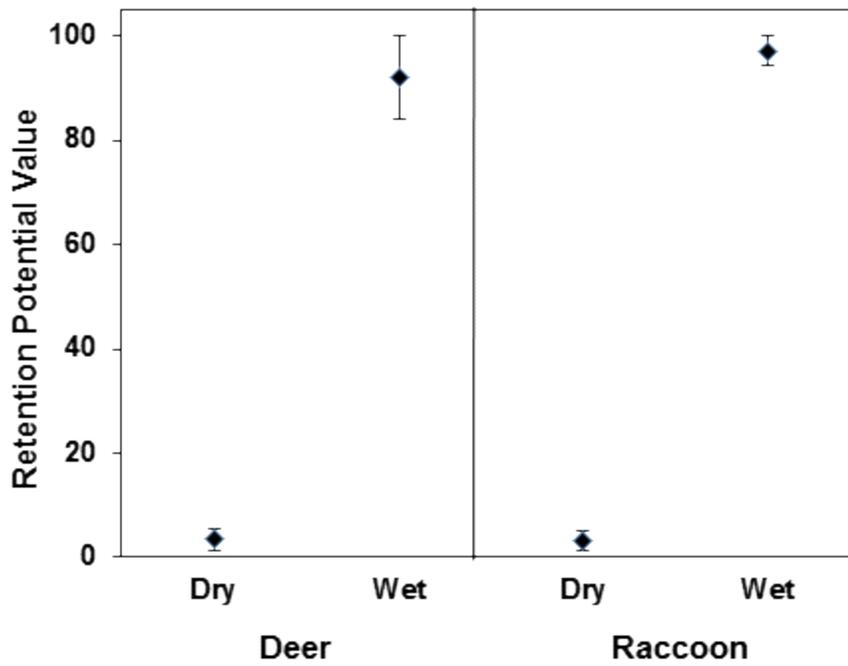


Fig. 3 The mean (\pm 95% CI) retention potential for the deer and raccoon pelts. The retention potential was significantly higher when the pelt was wet for both the deer and raccoon pelts. The 95% confidence intervals did not overlap with zero for any treatment.

CHAPTER II

EXPERIMENTALLY MEASURING SEED DISPERSAL DISTANCES TO
ESTIMATE THE DISPERSAL KERNEL OF THE INVASIVE PLANT, *ALLIARIA*
PETIOLATA

Abstract

Propagule pressure is important for the establishment and persistence of invasive species. Invasion success generally increases as propagule pressure increases. For the invasive plant *Alliaria petiolata*, propagule pressure is the most reliable predictor of invasion success; however, the model that estimated propagule pressure amounts was based on untested estimates of seed dispersal distances. Experimentally derived estimates of dispersal distances will provide more accurate estimates of propagule pressure than untested methods, which could lead to new insights regarding propagule pressure in *A. petiolata* invasion. We measured dispersal distances by placing seeds traps in a sector design around three seed point sources, which consisted of 15 second-year plants transplanted within a 0.25m radius circle. Traps were placed at intervals ranging from 0.25-3.25m from the point source. Trap number per interval increased with distance to maintain a constant sampling area. Traps were in the field until the majority of seeds were dispersed. Eight probability density functions describing dispersal distances of seeds from the point sources were fitted to seed trap counts via maximum likelihood. The lognormal and 2Dt functions had the best fit to the data and were selected for further

analyses. The lognormal and 2Dt predicted that seed density rapidly declined as distance increased with a mean dispersal distance of 0.56 and 0.52m and 95% of seeds dispersed within 1.22 and 1.14m for the two equations respectively. These results are the first to provide experimentally derived estimates of dispersal distances of *A. petiolata* and will improve our understanding of its invasive ability.

Introduction

Propagule pressure, also termed introduction effort, is recognized as one of the most important factors for explaining the ability of a species to invade a new area (Lockwood et al. 2005; Von Holle and Simberloff 2005; Simberloff 2009). Propagule pressure is defined as the total number of individuals of a species that are introduced into an area for which they are not native (Johnston et al. 2009). Invasion success of a species increases as propagule pressure increases (Kolar and Lodge 2001; Ahlroth et al. 2003; Blackburn et al. 2013). High propagule pressure can increase the genetic diversity of an established population (Huttanus et al. 2011), and the probability that some of the invading individuals will find suitable microhabitats within the invaded environment (Sax and Brown 2000; Warren et al. 2011), and ensure the established population is large enough to overcome demographic and environmental stochasticity (Veltman et al. 1996). High propagule pressure can also mitigate the risk that Allee effects (Taylor and Hasting 2005; Drake and Lodge 2006), inbreeding depression, and genetic drift (Simberloff 2009; Hufbauer et al. 2013) pose to successful long-term establishment. Because of its overwhelming importance, propagule pressure is now considered to be the null hypothesis for explaining invasion success (Colautti et al. 2006). Therefore, it is crucial that propagule pressure is accurately measured and accounted for in studies that explore

the invasion ability of a species (Chytry et al. 2008; Hufbauer et al. 2013; Brockeroff et al. 2014; Miller et al. 2014).

Propagule pressure plays an important role in the invasion success of the biennial, herbaceous, woodland plant *Alliaria petiolata*, garlic mustard, (Brassicaceae: Bieb. [Cavara & Grande]). However, many studies that attempt to explain *A. petiolata* invasion success have focused on its autecology (Anderson et al. 1996; Byers and Quinn 1998; Hillstrom and Cipollini 2011), competitive ability (Meekins and McCarthy 1999; Stinson et al. 2007; Bauer et al. 2010; Davis et al. 2012), or the habitat properties of sites it has invaded (Meekins and McCarthy 2001; Myers et al. 2005; Winterer et al. 2005). While these factors influence *A. petiolata* invasion success, they were far less important than propagule pressure in determining its invasion success (Eschtruth and Battles 2009, 2011). Nevertheless, a lack of information about certain components of its biology limits our ability to accurately measure propagule pressure for this species (Eschtruth and Battles 2009, 2011, 2014). Only certain aspects of propagule pressure in *A. petiolata* have been intensively studied, such as factors influencing seed production (Byers and Quinn 1998; Susko and Lovett-Doust 1998; Meekins and McCarthy 2001; Chapman et al. 2012). Other features, such as seed dispersal distances, have not been experimentally studied (Barney and Whitlow 2008), which limits our ability to accurately estimate propagule pressure. Filling this knowledge gap is essential if propagule pressure is to be accurately measured and its importance determined.

Other studies exploring *A. petiolata* invasion success have developed a model to measure propagule pressure, but the accuracy of this model may be unreliable due to a lack of experimental data regarding seed dispersal distances (Eschtruth and Battles 2009,

2011, 2014). Eschtruth and Battles (2009) estimated propagule pressure by measuring seed bank germination rates and developing the seed rain index shown below, to estimate the amount of seed rain dispersing into their research plots.

$$SR = \sum_{n=1}^N \text{fecundity} \times e^{(-b)\text{distance}} \quad \text{eqn. 1}$$

Where N is the total number of plants within a designated area, fecundity is the number of seeds produced per plant, *distance* is the distance between each plant and the area being considered, and b is the dispersal coefficient for the negative exponential dispersal function. The parameter value for fecundity was set at 156 seeds and was based on the work of three studies and is well supported (Anderson et al. 1996; Byers and Quinn 1998; Nuzzo 1999). The value of b was based on the assumption that 95% of seeds fall within the maximum reported distance of dispersal. The authors based their maximum dispersal distance on Nuzzo (1999), who suggested that a majority of seeds fall within one to two meters of the parent plant. However, since seed dispersal distances were not the focus of Nuzzo (1999), the distance of two meters was based on observations and simple field tests (Victoria Nuzzo personal communication), not experimental data. Lack of experimental data could result in the distance of two meters being in error. If the assumed dispersal distances are inaccurate, models based on these dispersal distances will provide an unreliable estimation of the seed rain and, therefore, propagule pressure. Experimentally measuring seed dispersal distances in the field should improve our estimation of seed rain and lead to a better estimation of propagule pressure for *A. petiolata*.

Accurately estimating seed dispersal distances is also important for improving current control strategies of *A. petiolata*. Elimination of established *A. petiolata*

populations requires intensive management, because eradication requires induced mortality rates greater than 85% of second-year plants over a span of several years for this biennial species (Pardini et al. 2009; Shyu et al. 2013). The success of these intensive efforts can be improved if the optimal spatial extent of control methods is calculated (Fletcher and Westcott 2013). If control efforts are focused on too small of an area, the efforts will be unsuccessful as the invasive species will disperse beyond the control area and infest new areas (Burgman et al. 2013). If the area under consideration is too large, then resources will be spread too thin and management efforts will not be intensive enough to eliminate the invasive species. Estimates of dispersal distances of *A. petiolata* can be used to determine the optimal spatial extent of control strategies to increase the success of management efforts. However, a small proportion of seeds are likely to be dispersed long distances through epizoochory (Chapter I) and establish satellite populations, but the primary advancing “front” of *A. petiolata* could be controlled and the rate of spread reduced.

An accurate estimate of the amount of seed rain entering research plots and the optimal spatial extent of control strategies can be determined through the calculation of a dispersal kernel (Robledo-Arnuncio and Garcia 2007). A dispersal kernel is a probability density function (pdf) that describes the dispersal of seeds from a parent plant (Clarke et al. 1999). There are two types of dispersal kernels, the dispersal location kernel, $g(r)$, and the dispersal distance kernel, $f(r)$ (Nathan et al. 2012). The $g(r)$ describes the probability of a seed dispersing into an infinitely small area at a distance from the parent plant and it can be used to predict the number of seeds that disperse to a specific area, such as a research plot, at a specific distance (Schurr et al. 2008). The $f(r)$ describes the probability

of a seed dispersing a specific distance, and it is useful for generating descriptive information about dispersal distances such as the median dispersal distance and distance at which 95% are dispersed within (Cousens et al. 2008). The number of seeds predicted to arrive in an area can be calculated through the following equation:

$$n = g(r)AQ \quad \text{eqn. 2}$$

where n is the expected seed count, $g(r)$ is the dispersal function evaluated at distance r from the point source, A is size of area under consideration, and Q is the total number of seeds dispersed. The density of dispersed seeds at a specific distance can be calculated by dividing both sides of the equation by A .

Dispersal kernels can be estimated by sampling seed density at increasing distances away from the seed source (Cousens et al. 2008). Typically a pdf is generated through the use of seed traps placed in a specific design around a seed source (Bullock et al. 2006). A mathematical function describing a $g(r)$ is fitted to the trap data to estimate the shape of the dispersal kernel. Assuming dispersal is isotropic, the same in all directions, the calculated $g(r)$ can be converted to the $f(r)$ with the equation:

$$f(r) = 2\pi r g(r) \quad \text{eqn. 3}$$

(Cousens and Rawlinson 2001). Estimating a $g(r)$ and $f(r)$ for *A. petiolata* can be used to calculate a more accurate prediction of the amount of seed rain entering an area, which will in turn provide a more accurate prediction of propagule pressure. The descriptive information generated from the $f(r)$ can be used to determine the spatial extent of control strategies.

The goal of this study was to generate a $g(r)$ and a $f(r)$ that describe the dispersal of *A. petiolata* seeds from the parent plant. Achieving this goal required capturing seed

rain with seed traps placed around three point sources of *A. petiolata* plants. Eight $g(r)$ functions were then fitted to the data and the best fitting functions were converted to an $f(r)$ through equation 2. The estimated $g(r)$ functions were analyzed to determine how quickly seed density decreases as distance from the point source increases. The predictions of the $g(r)$ functions were also compared to the predictions of the negative exponential function from Eschtruth and Battles (2009, 2011, 2014) to determine if they differed and how. In addition, the $g(r)$ functions were used to predict the number of seeds expected in a seed trap at varying distances away from the point sources. Lastly, the $f(r)$ was analyzed to generate descriptive data about seed dispersal distances. The mean, median, and distance at which 95% of seeds were dispersed within were all calculated.

Methods

Study Species

Alliaria petiolata is native to Eurasia occurring from England to Sweden to Turkestan, northwestern-Himalayas, India and Sri Lanka, and south to Italy and the Mediterranean basin (Tutin *et al.* 1964; Cavers *et al.*, 1979). The species was first recorded in North America on Long Island, New York in 1868 (Nuzzo 1993, Roberts and Anderson 2001). Since that time, it has spread exponentially and currently occurs in 37 states that stretch from the New England area to the west coast and five Canadian providences (USDA Plant Database). It is most abundant in northeastern United States and adjacent Canada in deciduous forests (Anderson *et al.* 1996). *Alliaria petiolata* is a member of the mustard family (Brassicaceae) and is a winter biennial. Germination occurs in late winter or early spring and basal rosettes are formed the first year. During early spring of the second year, plants bolt and rapidly increase shoot length with stem

elongation of 1.9 cm per day, between the 18 of April and the 13 of May (Anderson et al. 1996). Flowers form in March and April, while fruits develop in May and June. Seeds are dispersed from July to October with peaks occurring in August and September (Anderson et al. 1996). Baskin and Baskin (1992) found that 70% of seeds germinated in the first year under favorable conditions, but seeds can persist in the seed bank up to five years (Baskin and Baskin 1992).

Experimental Design

The study site for this research was the Parklands Foundation Merwin Nature Preserve, which is located 25 kilometers north of Normal, IL USA. The Merwin Nature Preserve is a 325 ha oak-hickory dominated second-growth forest that was protected from grazing since the 1970's. *Alliaria petiolata* seed point sources were established in areas that had minimal understory vegetation and nearly level topography. Sites were selected for these characteristics to minimize variation in dispersal distances due to the surrounding vegetation and gravity.

Each point source consisted of 15 second-year *A. petiolata* plants transplanted into a 0.25 m radius circle. Plants were transplanted during the late stages of fruit development just prior to the beginning of dehiscence. Since isolation is important for increasing the effectiveness of this experimental design (Bullock et al. 2006), all second-year *A. petiolata* plants within 9 m of the point source were removed. In the area beyond the 9 m, scattered *A. petiolata* plants occurred, but there were no dense stands. Dispersal was assumed to be isotropic (the same in all directions). To capture the seed rain, seed traps were placed at intervals of increasing distance around the point source in a sector design, which is the most effective design for isotropic dispersal (Skarpaas et al. 2005).

One sector was placed at every 45 azimuth degrees beginning at zero degrees north for a total of eight sectors. Within a sector, traps were placed at distances 0.25, 0.5, 0.75, 1.25, 2.25, 3.25 m from the center of the point source. In each sector, one trap was placed at distances 0.25, 0.50, and 0.75 m, two traps at 1.25 m, four at 2.25 m, and six at 3.25 m from the point source. The number of traps increased as distance from the point source increased to maintain a constant sampling effort (constant area sampled) per unit of circumference, but the number of traps was not increased until after 0.75 m to keep the total quantity of traps to a feasible number (Bullock and Clarke 2000).

Seed traps consisted of two plastic cups that had a diameter of 9.5 cm and a height of 12 cm. One cup was placed inside the other and nylon cloth was placed between the cups. Several small holes were inserted into the bottom of both cups. The holes allowed water drainage while the cloth captured the seeds. Each trap was placed in a hole slightly larger than the cup's diameter and deep enough so the top of the trap was flush with the ground surface. At distances with more than one trap, traps were placed so each touched its neighbor and all were equidistant from the center of the point source. For each point source, there were a total of 120 traps for 0.855 m² of trapping area.

Seed traps were placed around one point source in summer 2013 (Point Source 1) and two point sources in 2014 (Point Sources 2 and 3) at MNP. Traps were placed around the point source before the siliques began dehiscence and were collected after the vast majority of seeds dispersed. Traps were in the field from July 24th to October 5th and July 12th to August 28th for 2013 and 2014, respectively. After the seed traps were collected, the numbers of seeds in each trap were counted in the laboratory at Illinois State University.

The total number of seeds dispersed from a point source was estimated by subtracting the number of seeds that were not dispersed from point source at the end of the experiment, from the estimated total at the beginning. To estimate the initial total number of seeds in a point source, the length of each silique was measured and the number of seeds inside was estimated with the equation $S = -6.8 + 4.38x$ ($F_{1,138} = 419.5$, $p < 0.0001$, $R^2 = 0.752$). S is seed number and x is silique length in cm (Anderson unpublished data). When seed traps were collected, the siliques remaining in the point source were also collected and the seeds within them were counted in the laboratory.

Seed count data were used to estimate the parameters of eight different $g(r)$ dispersal functions (Table 3) that are described in Nathan et al. (2012). These functions include a scale parameter (a) and a shape parameter (b) except for the gaussian and negative exponential, which only have the a parameter. Since dispersal was assumed to be isotropic, direction was ignored when fitting the $g(r)$ functions. While there was variation in seed counts among the directions, there was no consistent pattern. Also, assuming isotropic dispersal allows for more general predictions about dispersal distances to be made than if directions were analyzed separately. Lastly, there are no known *a priori* reasons for why directions would differ.

The $g(r)$ functions were fitted to the seed count data using equation 2. The parameter n was the seed number captured by a trap, $g(r)$ was one of the eight functions evaluated at distance r , A was the area of a seed trap (0.007125 m^2), and Q was the estimated number of seeds within the point source around which the trap was located. Parameter values for the dispersal functions were estimated by non-linear mixed effects modelling which minimizes the negative log-likelihood value ($-\ln L$) using maximum

likelihood (PROC NLMIXED) in SAS[®] software 9.3 (SAS Institute 2012). The default quasi-Newton algorithm was used. The product AQ was included as an offset variable as suggested by Cousens et al. (2008). Offset variables do not have a coefficient value estimated. An additional random effect parameter (u) was included to account for random variation among the point sources.

Each dispersal function was fitted to the data using a log-link function and a negative binomial error distribution. Functions were also fitted with a Poisson distribution, but in all cases the negative binomial had a better fit. The negative binomial distribution assumes seeds are distributed with a mean of N and the dispersion parameter k , which accounts for over dispersion (Clark et al. 2005). The dispersal function with the lowest Akaike Information Criterion (AIC) score was selected for all further analysis. The AIC score was calculated as $-2 \ln L + 2K$ where K is the number of fitted parameters. The $-2 \ln L$ measures how well the model fits the data while $2K$ is a correction factor to account for model complexity (Johnson and Omland 2004).

The selected $g(r)$ was evaluated to ensure that it met the requirements of a pdf. These requirements are that the function must be positive over the entire expressed space and the function must integrate to one (Cousens and Rawlinson 2001). The graphical representation of the $g(r)$ was visually inspected to ensure the function was positive and the integral was calculated as described by Nathan et al. (2012):

$$\int_0^{\infty} \int_0^{2\pi} g(r)r drd\theta = 1 \quad \text{eqn. 4}$$

where θ ranges from 0 to 2π and r ranges from 0 to $+\infty$. If the $g(r)$ met the requirements of a pdf, it was then converted to the $f(r)$ with equation 2. The $f(r)$ is also a pdf and must

meet the requirements. Again, the graphical representation of $f(r)$ was inspected to determine if the function was positive, and the integral was calculated with the equation:

$$\int_0^{\infty} 2\pi r g(r) dr = 1 \quad \text{eqn. 5}$$

(Peart 1985). If the $g(r)$ and $f(r)$ did not meet the requirements of a pdf, then the $g(r)$ and corresponding $f(r)$ were not used for analysis. Alternatively, the $g(r)$ and resultant $f(r)$ with the lowest AIC score, and that met the requirements of a pdf, were selected. The integrals were calculated using the Wolfram|Alpha online integral calculator (<http://www.wolframalpha.com>).

The selected $g(r)$ was analyzed to determine how quickly the probability of a seed being dispersed into an infinitely small area decreased as distance from the point source increased. The $g(r)$ was also placed into equation 2 to predict the expected number of seeds per trap at each distance for each of the three point sources. These predictions were then compared to the actual seed counts from the field. The selected $g(r)$ function was compared to the negative exponential from Eschtruth and Battles (2009) by using both functions to predict the change in dispersed seed density as distance increased from a single second-year *A. petiolata* plant. The fecundity of *A. petiolata* plants was set to 156 seeds as this was the fecundity value used in Eschtruth and Battles (2009). The $f(r)$ was analyzed to calculate the median dispersal distance and the distance at which 95% of seed are dispersed by determining the distance at which the $f(r)$ integrated to 0.50 and 0.95, respectively.

Results

The estimated number of seeds released from the three point sources was 4012, 4020 and 4815 for Point Sources 1, 2, and 3, respectively. The total number of seeds captured in the point sources and the percentage that was of the total was 384 (9.57%), 629 (15.65%), and 682 (14.16%) for Point Sources 1, 2, and 3, respectively. In all three point sources, the mean number of seeds captured per trap was highest in traps placed at distance 0.25 m, and then the mean number of seeds captured per trap steadily decreased as distance from the point source increased (Table 4). Point Source 1 had the lowest average number of seeds per trap at distance 0.25 m with $23.4(\pm 6.47)$ seeds per trap and Point Source 2 had the highest with $49.6(\pm 10.51)$ seeds per trap. A small number of seeds were dispersed 2.25 m with all three Point Sources averaging below one seed per trap. Even fewer seeds were dispersed 3.25 m with all point sources averaging below 0.5 seeds per trap (Table 4).

The AIC scores of the eight $g(r)$ dispersal functions fit ranged from 1008.8 to 1033.5. The Weibull function had the lowest AIC score, but the $g(r)$ and $f(r)$ functions did not integrate to one. Therefore, the Weibull did not meet the requirements of a pdf. Because of the Weibull not meeting the pdf requirement, the lognormal function was selected for analysis since it had the next lowest AIC score at 1020.4 and the $g(r)$ and $f(r)$ met the requirements of a pdf. The $g(r)$ of the lognormal function predicted that the probability density of a seed dispersing into an infinitely small area was zero at distance zero, and then it rapidly increased, peaked at 0.25 m, and then declined beyond 0.25 m (Fig. 4). However, field observations indicate many seeds fall directly below the parent

plant which would result in the density probability being greater than zero at distance zero.

To address this difference between the lognormal dispersal kernel and field observations, the 2Dt function was also analyzed. The 2Dt kernel had the next lowest AIC score after the lognormal at 1025.5 and the $g(r)$ and $f(r)$ met the requirements of a pdf. The 2Dt $g(r)$ kernel predicted that the probability density of a seed landing in an infinitely small area is highest at distance zero and then steadily declines until one meter (Fig. 4). This result is more in agreement with observations from the field and is different than the lognormal. However, beyond 0.25 m, the two $g(r)$'s have a similar shape with both probability densities rapidly declining as distance increases to one meter. As the distance increased beyond one meter, the probability density for both functions asymptotically approach zero.

The differences in the $g(r)$'s for both functions are also apparent when they are placed into equation 1 to predict the seed counts per trap. Counts from each of the three point sources were analyzed separately. Mirroring the $g(r)$, the lognormal function predicts that the seed count per trap is zero at distance zero, and then the count rapidly increases until it peaks at 0.25 m (Fig. 5). The predicted counts then decline until less than one seed per trap is predicted beginning at 1.30 m. The 2Dt function predicts that the seed count per trap is highest at 0 m and then the predicted count steadily decreases until 1.30 m, where again less one seed per trap is predicted. For both functions, the predicted seed count per trap continues to decrease beyond 1.30 meters asymptotically approaching zero.

The predicted change in dispersed seed density from a single second-year plant of the lognormal and 2Dt $g(r)$ functions differs from the prediction of the negative exponential function from Eschtruth and Battles (2009). Specifically, the negative exponential function predicts dispersed seed density to be higher than the lognormal and 2Dt functions beginning at 0.5 m and beyond from the point center (Fig. 6). The higher predicted dispersed seed density of the negative exponential function indicates that the function is over estimating the amount of seed rain landing at 0.50 meters and at further distances when compared to the lognormal and 2Dt $g(r)$ functions.

The corresponding $f(r)$'s of the lognormal and 2Dt functions also have differences, but the differences are less pronounced. Both $f(r)$'s have a probability density of zero at distance zero, which is a condition any $f(r)$ will meet due to the multiplier r equaling zero at distance zero in equation 5. The largest difference between the two $f(r)$'s occurs between 0 and 0.25 m (Fig. 7). The probability density of the 2Dt function increases more rapidly than the lognormal function, which reflects the 2Dt function predicting more seeds being dispersed to this interval than the lognormal (Fig. 5). While the lognormal increases less rapidly than the 2Dt function, the probability density of both functions peak at 0.35 m, meaning seeds have the highest probability of dispersing to this distance. Both functions steadily decline from this peak with the lognormal declining slightly less rapidly due to more seeds being dispersed between 0.35 and 1.20 meters than the 2Dt. The mean and median dispersal distances were similar between the two functions. The mean and median dispersal distance and the distance at which 95% of seeds were dispersed within was 0.56 m, 0.53 m, and 1.22 m for the lognormal function and 0.53 m, 0.47 m, and 1.14 m for the 2Dt function

For the lognormal and 2Dt functions, the variation in seed counts within the traps attributable to differences among the point sources was not significant, due to the parameter u not being significantly different than zero (Table 5). For both functions, the k parameter was less than one. If k is less than one, this result indicates that there is a high amount of variation around the expected values (Clark et al 2005). The high variation is apparent when observing the predicted seed counts per trap of the dispersal functions to the actual seed counts from the traps in the field (Fig. 5). There was a large amount of variability in the number of seeds captured at distances 0.25 and 0.5 m. At the 0.25 m distance, captured seeds varied from as few as 3 seeds to as many as 117 seeds per trap, and at the 0.5 m distance they varied from 2 to 59.

Discussion

The results from this experimental study provide a more accurate and precise prediction of dispersal distances in *A. petiolata* than those available in the literature (Nuzzo 1999; Drayton and Primack 1999), which are based on observational information. The lognormal and 2Dt functions predict that the majority of seed dispersal is within one meter of the parent plant with peak dispersal occurring around 0.35 m and 95% of seeds dispersed within 1.22 and 1.14 m, respectively. Both functions predict that the distance at which 95% of seeds are dispersed is about 0.80 m less than the two meters used to estimate the value of the b parameter of the negative exponential function used by Eschtruth and Battles (2009, 2011, 2014). Our results suggest that the value of b is an imprecise estimate, and as a result, the negative exponential function is overestimating seed dispersal distances. The overestimation of dispersal distances is also apparent when the predicted dispersed seed density of the negative exponential function is compared to

that of the lognormal and 2Dt functions (Fig. 6). The negative exponential is overestimating the dispersed seed density at distances of 0.50 m and greater. By overestimating dispersal distances, the seed rain index of Eschtruth and Battles (2009, 2011, 2014) also overestimated the amount of seed rain entering their research plots, which resulted in an over estimation of propagule pressure. Incorporating the experimentally based dispersal functions from this study will improve the accuracy of estimates of seed rain, and therefore, propagule pressure.

To obtain an accurate estimate of the amount of seed rain entering research plots, researchers can choose from either the lognormal or 2Dt dispersal kernel. The amount of seed rain entering a research plot can be estimated by replacing the negative exponential function in equation 1 with the $g(r)$ of either the lognormal or 2Dt function and then multiplying by the area of the research plot (Skarpaas et al. 2004). Researchers can select the $g(r)$ that they believe is the most appropriate for their study. The 2Dt might be a better choice if distances less than 0.25 m are being considered, while the lognormal might be more appropriate for distances greater than 0.25 m. However, using the $g(r)$ in equation 1 may result in an unreliable estimate of seed rain if the area of the research plot is much larger than the area of a single seed trap used in this study. An unreliable estimate arises because the probability densities of the dispersal curves rapidly change over small changes in distance (Fig. 4 and 7). The rapid change in probability density causes the predicted seed count to also rapidly change over this distance (Fig. 5). Therefore, if the research plot is large enough, the predicted seed count could vary significantly across the area of the research plot. This variation needs to be accounted for to generate a more accurate estimate of amount of seed rain.

An alternative method for calculating the seed rain entering a research plot is to use integration to calculate the number of seeds dispersed into the annulus that contains the research plot, and then multiplying this number by the proportion of the annulus covered by the research plot (Clark et al. 1999). The points of the plot that are the farthest (r_{max}) and nearest (r_{min}) to the seed source define the size of the concentric rings that bound the annulus within which the research plot lies within. Integration is then used to calculate the number of seeds dispersed into this annulus. The number of seeds dispersed into the annulus is multiplied by the proportion of the annulus covered by the research plot to calculate the number of seeds dispersed into the research plot (Poulsen et al. 2012). This function is displayed in the following equation:

$$N = \left(\int_{r_{min}}^{r_{max}} \int_0^{2\pi} g(r)r drd\theta \right) * \frac{A}{\pi(r_{max})^2 - (r_{min})^2} \quad \text{eqn. 6}$$

where N is the proportion of seeds dispersed that fall into the research plot. Equation 6 can replace the negative exponential function in equation 1 which will result in a more accurate prediction of the amount of seed rain entering research plots as it accounts for changes in predicted seed counts across the area of the research plot.

The information about dispersal distances generated from this study can also be used to inform management decisions to prevent the local spread of established *A. petiolata* populations. To prevent the spread of invasive species, the key drivers of spread must be identified and management strategies must address these drivers (Caplat et al. 2012). For species with similar life cycles to *A. petiolata*, the mean dispersal distance is an important driver for the spread of established populations and control efforts need to focus on preventing dispersal (Coutts et al. 2011). One method of preventing dispersal is

targeted surveillance and removal of second-year plants that are derived from dispersed seeds. Because annual mortality rates of >85% of second-year plants are required over several years to eradicate established *A. petiolata* populations (Pardini et al. 2009; Shyu et al. 2013), it is important that the surveillance efforts identify >85% of dispersed seeds that develop into adult plants. The dispersal distances from this study can be used to define the spatial scale of the surveillance efforts. Surveillance efforts should include the area of the established population and an additional 1.14-1.22 m beyond the edge of the population as this would encompass 95% of dispersed seeds as predicted by the 2Dt and lognormal functions (Table 5). Since these distances are relatively small, the surveillance area could be increased with little additional effort. The targeted surveillance distance of 1.14-1.22 m will not detect the 5% of seeds that are dispersed beyond this distance. Since these seeds are important for the establishment of satellite populations, different control strategies are required to address the dispersal seeds beyond 1.14-1.22 m.

The relatively short dispersal distances predicted from the lognormal and 2Dt functions indicates the presence of a long distance dispersal mechanism for *A. petiolata*. Similar to other plant species, the vast majority of *A. petiolata* disperse a very short distance from the parent plant (Clarke et al. 2005) resulting in a thin tail of the $f(r)$'s dispersal kernels (Fig. 7). The thin tail indicates that very few seeds are dispersed long distances (Levin et al. 2003). Despite few seeds being dispersed long distances, *A. petiolata* was observed to spread at a rate of 5.4 m per year (Nuzzo 1999), and it also spreads through the establishment of satellite populations that become established well ahead of the invasion front (Nuzzo 1993, 1999; Burls and McClaugherty 2008). The rapidly moving invasion front and establishment of satellite populations indicate that an

unknown mechanism is dispersing a small proportion of *A. petiolata* seeds to distances greater than those measured in this study.

The mechanism of long distance dispersal for *A. petiolata* is not readily apparent as it lacks any clear adaptations that favor long distance dispersal (Hintze et al. 2013). However, epizoochory (external animal transport) has been suggested (Cavers et al. 1979; Blossey 2001; Evans et al. 2012). Experimental data has demonstrated that animals transport seeds in the field and that a small proportion of *A. petiolata* seeds are able to attach and be retained within the fur of mammals, providing evidence that epizoochory is a likely long distance dispersal mechanism (Chapter I). Seeds of many plant species are dispersed long distances even though they have no apparent adaptations for long distance dispersal, as seen in *A. petiolata* (Higgins et al. 2003; Nathan 2006). Therefore, to understand the spread of *A. petiolata* across the landscape, the short distance dispersal described in this study should be combined with the potential long distance dispersal due to epizoochory. The short distance dispersal is likely important for the spread of established populations (Coutts et al. 2011), while the long distance dispersal is needed for the establishment of new satellite populations (Clark et al. 1998; Cain et al. 2000).

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Table 3. The eight $g(r)$ dispersal functions as described in Nathan et al. (2012) that were fitted to the seed trap data. The parameter a is a shape parameter and b is a scale parameter which determines the relative weight of long distance dispersal events, and r is the distance from the center of the point source.

Function	$g(r)$
Negative Exponential	$\frac{1}{2\pi a^2} \exp\left(-\frac{r}{a}\right)$
Log Normal	$\frac{1}{2\pi^{3/2} b r^2} \exp\left(-\frac{\log\left(\frac{r}{a}\right)^2}{2b^2}\right)$
2Dt	$\frac{(b-1)}{\pi a^2} \left(1 + \frac{r^2}{a^2}\right)^{-b}$
Weibull	$\frac{b}{2\pi a^2} r^{b-2} \exp\left(-\frac{r^2}{a^b}\right)$
Gaussian	$\frac{1}{\pi a^2} \exp\left(-\frac{r^2}{a^2}\right)$
Logistic	$\frac{b}{2\pi a^2 \Gamma(2/b) \Gamma(1-2/b)} \exp\left(1 + \frac{r^b}{a^b}\right)^{-1}$
Exponential Power	$\frac{b}{2\pi a^2 \Gamma(2/b)} \exp\left(-\frac{r^b}{a^b}\right)$
(Inverse) Power-Law	$\frac{(b-2)(b-1)}{2\pi a^2} \left(1 + \frac{r}{a}\right)^{-b}$

Table 4. The average number of seeds (\pm SE) captured in a single trap at each distance for all three point sources.

D	Source 1	Source 2	Source 3
0.25	23.4 (\pm 6.47)	49.6 (\pm 10.51)	39.7 (\pm 11.32)
0.5	11.2 (\pm 5.52)	16.7 (\pm 3.27)	26.0 (\pm 6.64)
0.75	4.8 (\pm 1.44)	7.8 (\pm 1.24)	7.9 (1.96)
1.25	1.6 (\pm 0.43)	1.3 (0.36)	0.46 (\pm 0.210)
2.25	0.84 (\pm 0.147)	0.22 (0.088)	0.16 (\pm 0.066)
3.25	0.46 (\pm 0.104)	0.19 (0.063)	0.12 (\pm 0.054)

Table 5. The parameter estimates and their standard errors of the lognormal and 2Dt functions. k is an extra parameter in the negative binomial distribution that accounts for over dispersion. The random variation due to differences among point sources (u) was not significant.

Function	Parameter	Estimate	St. Err	DF	p-value
Lognormal	a	0.4789	0.02222	2	0.0021
	b	0.5647	0.04557	2	0.0065
	u	0.1412	0.1229	2	0.3694
	k	0.6141	0.1021	2	0.0265
2Dt	a	1.0561	0.3427	2	0.0911
	b	4.8795	2.1794	2	0.1545
	u	0.1474	0.1282	2	0.3692
	k	0.6493	0.1062	2	0.0257

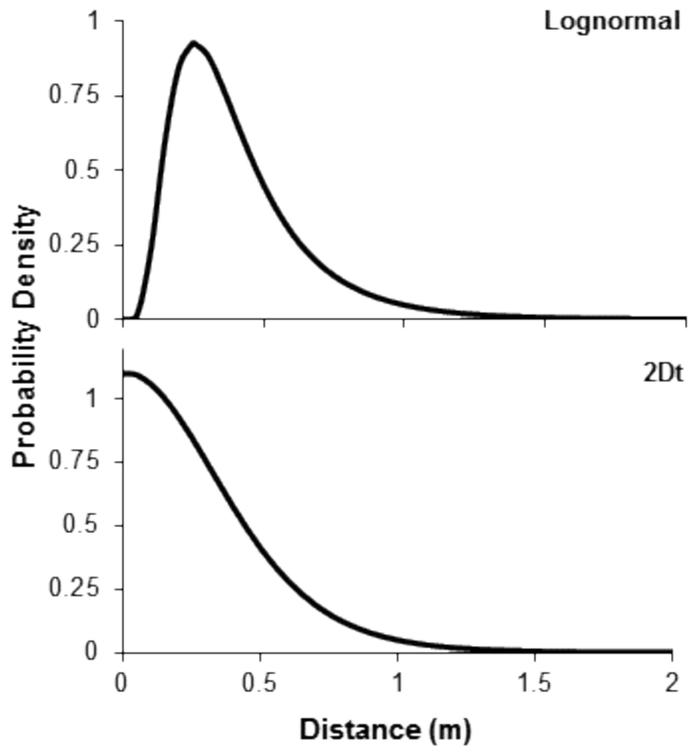


Fig. 4 The density pdf ($g(r)$) of the lognormal and $2Dt$ functions. The $g(r)$ describes the probability of a seed landing into an infinitely small area at a specific distance from the point source.

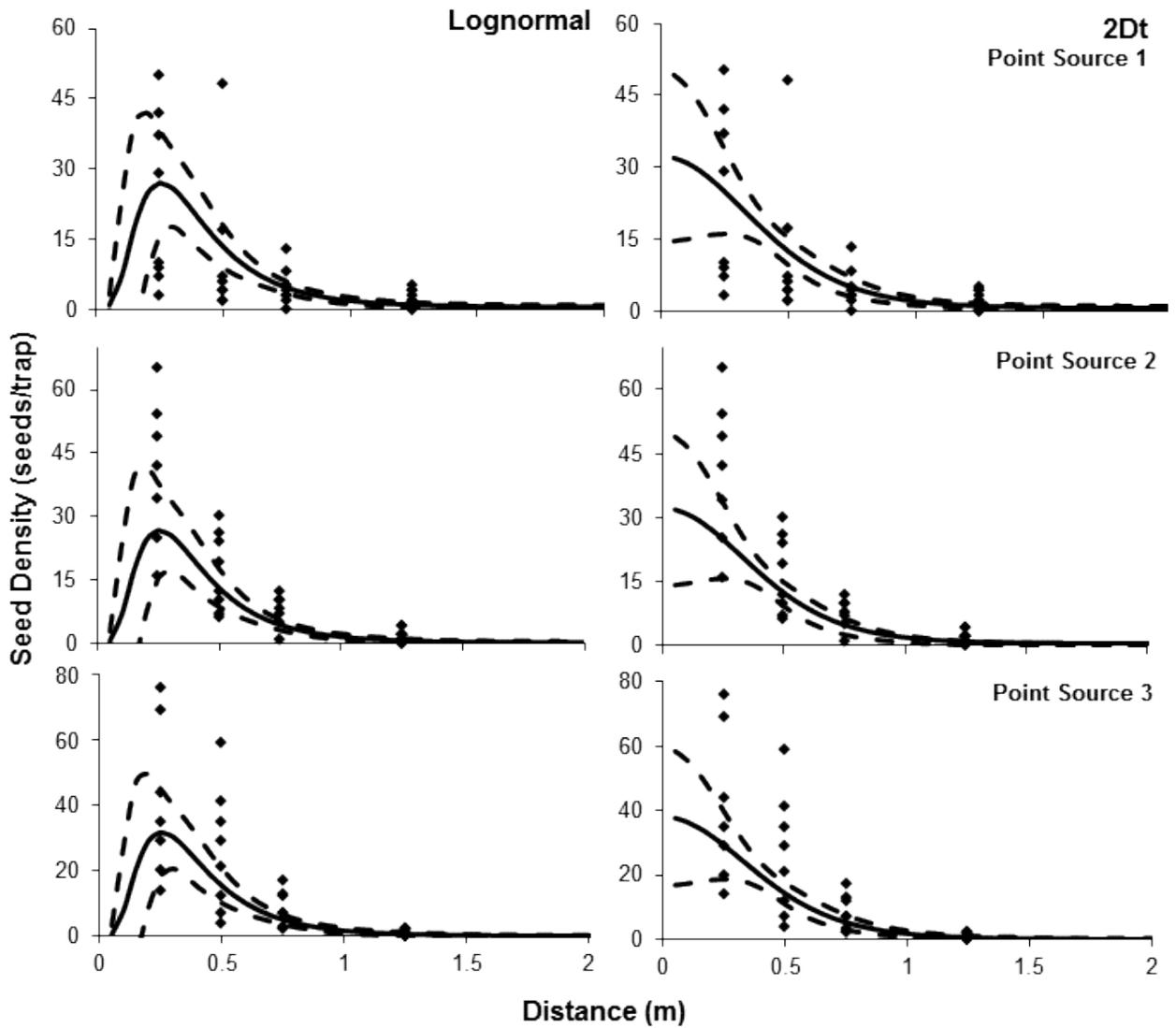


Fig. 5 The predicted seed count per trap (solid line) \pm 95% confidence intervals (dashed lines) for the lognormal and 2Dt functions. Each of the point sources was plotted separately and the black diamonds are the seed counts from the seed traps.

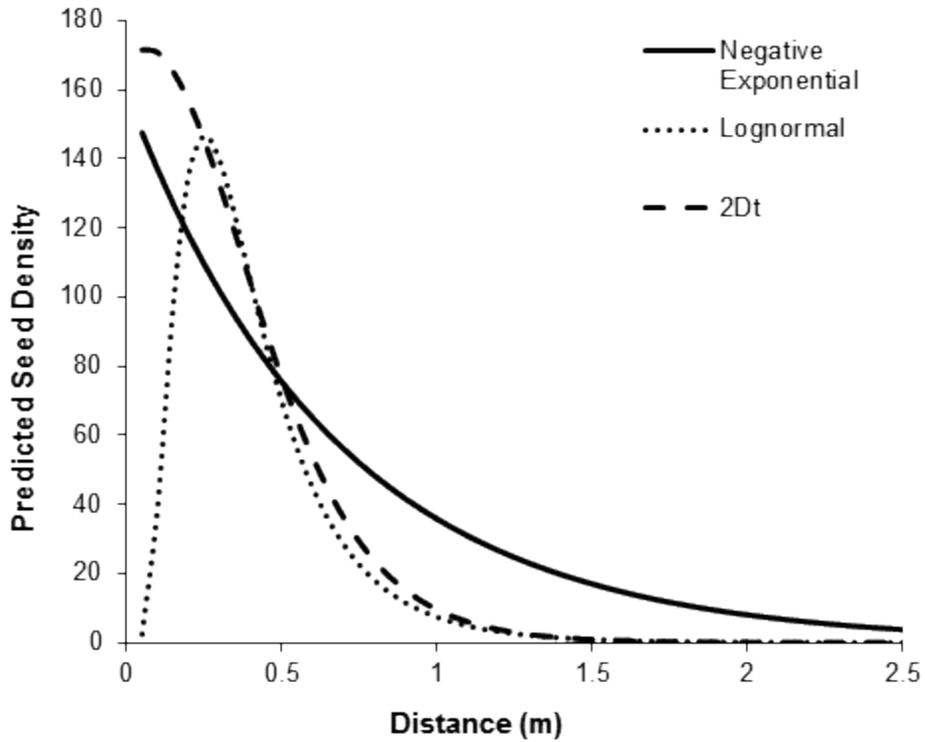


Fig. 6 The change in predicted seed density as distance from the parent plant increases as predicted by the negative exponential function from Eschtruth and Battles (2009) and the lognormal and 2Dt $g(r)$ functions. The fecundity of the parent plant was set to 156 seeds as this was the value used by Eschtruth and Battles (2009). Beginning at 0.50 meters, the negative exponential overestimates the dispersed seed density compared to the lognormal and 2Dt $g(r)$ kernels.

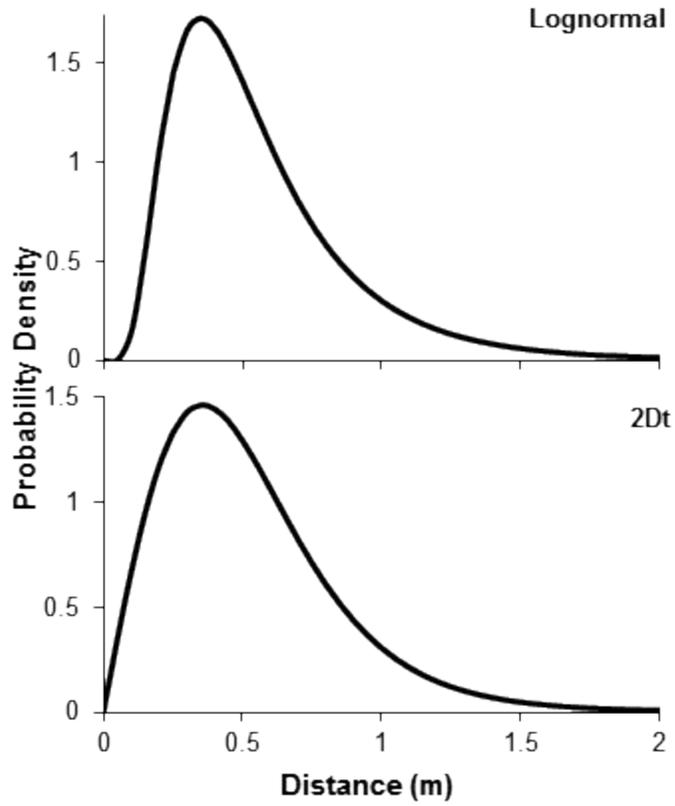


Fig. 7 The distance pdf ($f(r)$) of the lognormal and $2Dt$ functions. The $f(r)$ describes the probability of a seed dispersing to a specific distance from the point source.