

1 Measuring short distance dispersal of *Alliaria petiolata* and determining potential long-distance
2 dispersal mechanisms.

3 Christopher A. Loebach¹ and Roger C. Anderson¹

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8 **Affiliation for Authors:**

9 Illinois State University

10 School of Biological Sciences

11

12 **Address for Authors:**

13 School of Biological Sciences

14 Illinois State University

15 Normal IL, 61790-4120

16

17

18 **Corresponding Author**

19 Christopher A. Loebach

20 Email:chris_loebach@yahoo.com

21 Phone number: **515-884-8201**

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Abstract

Introduction: *Alliaria petiolata*, an herbaceous plant, has invaded woodlands in North America. Its ecology has been thoroughly studied, but an overlooked aspect of its biology is seed dispersal distances and mechanisms. We measured seed dispersal distances in the field and tested if epizoochory is a potential mechanism for long-distance seed dispersal.

Methods: Dispersal distances were measured by placing seed 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. Traps remained in the field until a majority of seeds were dispersed. Eight probability density functions were fitted to seed trap counts via maximum likelihood. Epizoochory was tested as potential seed dispersal mechanism for *A. petiolata* through a combination of field and laboratory experiments. To test if small mammals transport *A. petiolata* seeds in their fur, experimental blocks were placed around dense *A. petiolata* patches. Each block contained a mammal inclusion treatment (MIT) and control. The MIT consisted of a wood-frame (31x61x31cm) covered in wire mesh expect except for the two 31x31cm ends. The frame was placed over a germination tray filled with potting soil. A pan filled with bait was placed in the center of the tray. The control frame (11x31x61cm) was placed over a germination tray and completely covered in wire mesh to exclude animal activity. Treatments were in the field for peak seed dispersal. In March, trays were moved to a greenhouse and *A. petiolata* seedlings were counted and then compared between treatments. To determine if *A. petiolata* seeds attach to by raccoon (*Procyon lotor*) and white-tailed deer (*Odocoileus virginianus*) fur, wet and dry seeds were dropped onto wet and dry fur. Furs were rotated 180 degrees and the seeds that remained attached were counted. To measure seed retention, seeds were dropped on furs and rotated as before. Then the furs were agitated for one hour. The seeds retained in the fur were counted.

Results: For the seed dispersal experiment, the 2Dt function provided the best fit and was the most biologically meaningful. It predicted that seed density rapidly declined as with distance from the point source increased. Mean dispersal distance was 0.52m and 95% of were-seeds dispersed within 1.14m. The epizoochory field experiment showed increased mammal activity and *A. petiolata* seedlings in germination trays of the MIT compared to control. Laboratory studies showed 3-26% of seeds were attached and were-retained by raccoon and deer fur. Retention significantly increased if either seed or fur were wet (57-98%).

Discussion: Without animal seed vectors, most seeds fall within a short distance of the seed source; however, long distance dispersal may be accomplished by epizoochory. Our data are consistent with explain *A. petiolata*'s widespread distribution and development of dense clusters of the species in invaded areas.

Introduction

Alliaria petiolata, garlic mustard (Brassicaceae: Bieb. [Cavara & Grande]), is an herbaceous invasive species that has invaded woodlands in eastern North America (Anderson et

68 *al.* 1996). *Alliaria petiolata* is native to Eurasia, occurring from England to Sweden to Turkestan,
 69 northwestern-Himalayas, India and Sri Lanka, and south to Italy and the Mediterranean basin
 70 (Tutin *et al.* 1964; Cavers *et al.* 1979). It also occurs outside of its native range in Australia
 71 (CAB International 2015, EDDMapS 2015). The species was first recorded in North America on
 72 Long Island, New York in 1868 where it was introduced by humans as a food plant (Nuzzo
 73 1993, Roberts and Anderson 2001). Since that time, it has spread exponentially and currently
 74 occurs in 37 states that stretch from the New England area to the west coast and five Canadian
 75 providences (USDA Plant Database). It is classified as invasive in 20 U.S. states and in ~~all~~ five
 76 Canadian provinces [there are 10 Canadian provinces!] (CAB International 2015, EDDMapS
 77 2015).
 78 *Alliaria petiolata* has been extensively studied in an effort to understand its invasive
 79 ability and impact on native communities (Rodgers *et al.* 2008). To better understand *A.*
 80 *petiolata* invasive ability, studies have investigated the competition between *A. petiolata* and
 81 native plant species (Bauer *et al.* 2010, Phillips-Mao *et al.* 2014), the role of disturbance caused
 82 by *Lumbricus terrestris* and *L. rubellus* (Nuzzo *et al.* 2009), and the preferential browsing of
 83 white-tailed deer, *Odocoileus virginianus* on native species (Knight *et al.* 2009, Kalisz *et al.*
 84 2014). *A. petiolata* ~~Nevertheless, it~~ continues to invade new areas (Welk *et al.* 2002) and persists
 85 in areas where it has become established, although its abundance in invaded areas can decline
 86 over time (Davis *et al.* 2012, Lankau *et al.* 2009). A largely overlooked aspect of *A. petiolata*'s
 87 biology is seed dispersal distances and mechanisms (Barney and Whitlow 2008). Closing this
 88 knowledge gap is important for improving our understanding of the invasive ability of *A.*
 89 *petiolata* and how it disperses across the landscape.

Eschtruth and Battles (2009, 2011, 2014) studied *A. petiolata*'s ability to invade new areas and found that propagule pressure is the most important factor. The importance of propagule pressure was tested through a propagule pressure model. However, this model was built on untested dispersal distances assumptions and predicted that 95% of seeds fall within the maximum reported distance of dispersal of two meters as described in Nuzzo (1999) and Drayton and Primack (1999). The reported dispersal distances were based on observations and simple field tests (Nuzzo 1999, Dayton and Primack 1999, Victoria Nuzzo personal communication 2014), not experimental data. Therefore, it is possible that the importance of propagule pressure was not accurately estimated due to the parameters of the underlying model being based on untested assumptions. Experimentally measuring dispersal distances in the field may provide the basis for a more accurate estimate of propagule pressure and its importance in *A. petiolata* invasion.

If the vast majority of *A. petiolata* seeds are dispersed 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 per year, 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 suggest 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, epizoochory has been suggested as a possible dispersal mechanism (Blossey 2001, Cavers *et al.*,

and Evans *et al.* 2012) with deer, mice, and other small mammals possibly 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 ability of a seed to attach to fur (Will *et al.* 2007), and to be retained in the fur 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 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).

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 fur dampness did not have a consistent effect on the retention potential for all 19 species they tested, but dampness increased 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.

Our study had two objectives. The first objective was to experimentally measure *A. petiolata* seed dispersal distances in the field using seed traps and use these data to estimate the parameters of eight dispersal kernels. 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 given distance from the parent plant and it can be used to predict the number of seeds that are expected to land in a specific area at a specific distance from the seed source (Schurr *et al.* 2008). We compared the predictions of the $g(r)$ from our study to the negative exponential function used by Eschtruth and Battles (2009, 2011, 2014). The $f(r)$ describes the probability of a seed dispersing a specific distance, and was used to calculate median dispersal distance and distance at which 95% are dispersed within (Cousens *et al.* 2008) [\[Much of this paragraph \(and some of next\) would be better placed in Methods section\]](#).

Our second objective was to test the hypothesis that epizoochory via North American woodland mammals is a long distance seed dispersal mechanism ~~in~~^{of} *A. petiolata*. We 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 pelts. Our study is the first to experimentally measure *A.*

petiolata seed dispersal distances in the field and also to demonstrate that epizoochory is a probable long distance seed dispersal mechanism.

Methods

Study Species

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 up to 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 small [(mean $\pm$ SE, L x W, $3.6 \pm 0.05 \times 1.3 \pm 0.03$ mm), range L (3.1-4.5 mm) and W (0.9 -1.9 mm), N = 50] (Anderson unpublished data, Normal, IL, 2016) and Mullarkey *et al.* (2013) reported that seed mass varied from 2.11 ± 0.04 to 2.38 ± 0.034 depending upon cross type (e.g., within populations, between populations, or selfing). According to Anderson *et al.* (1996), seeds are dispersed from July to October with peaks occurring in August and September. 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 within two properties of the Parkland's Foundation, which were the Merwin Nature Preserve and South Breen's 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 livestock grazing since the 1970's. The South Breens Woods is a four ha oak dominated forest and has been under protection since 1979. At Parklands, the dominant tree species at study areas are

area Ohio buckeye (*Aesculus glabra*), hackberry (*Celtis occidentalis*), American elm (*Ulmus rubra*), yellowbud hickory (*Carya cordiformis*), and black walnut (*Juglans nigra*). The dominant ground layer species were wood nettle (*Laportea canadensis*), black snake root (*Sanicula odorata*), wing stem (*Verbesina alternifolia*), Virginia wildrye (*Elymus virginicus*), and Virginia creeper (*Parthenocissus quinquefolia*). At Breens Woods, the dominant tree species white oak (*Quercus alba*), American elm, red elm (*Ulmus rubra*), black cheery (*Prunus serrotina*), and iron wood (*Ostrya virginiana*). The dominant ground-layer species are Virginia creeper, Solomon seal (*Polygonatum commutatum*), false Solomon seal (*Smilicina racemosa*), jack in the pulpit (*Arisaema triphyllum*), and sweet-scented bedstraw (*Galium triflorum*). *Alliaria petiolata* was present and abundant at both sites as were other invasive species such as buckthorn (*Rhamnus cathartica*) and honeysuckle (*Lonicera maackii*). The mapped soil type of the Parklands site is straw loam (224C2) and the mapped soil type for Breens Woods is Birbeck silt loam (233B2) (Soil Survey of McLean County, Illinois, 2004). *[This section confusing and inefficient; perhaps something like, "Dominant tree species at both areas include....", then list additional species dominant at just one or the other. Then same for ground-layer species...]*

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Seed Trap Design

Our experiment was designed to determine the *A. petiolata* dispersed seed density at increasing distances away from the seed source and to use these data to estimate the parameters of the eight dispersal location kernels, $g(r)$ (Table 1) (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:

$$f(r) = 2\pi rg(r)$$

eqn. 1

(Cousens and Rawlinson 2001). *[some of methodological details from Intro should be moved to this paragraph.]*

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The seed dispersal study was conducted at ~~Parklands Foundation~~ Merwin Nature Preserve. *Alliaria petiolata* seed point sources were established in areas where there were no trees or shrubs within 3.5 meters, where understory vegetation cover was less than 20%, and where there was nearly level topography. Sites were also located within the interior of the woodlands with a full canopy. Sites were selected for these characteristics to minimize variation in dispersal distances due to the surrounding vegetation and gravity.

An *A. petiolata* seed point source consisted of 15 second-year *A. petiolata* plants transplanted into a single 0.25 m radius circle. The 15 plants were randomly located within the circle. In total, three point sources were created. 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 assessing isotropic dispersal (Skarpaas *et al.* 2005). One sector consisted of ~~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, 0.50, 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 (Fig. 1). The

227 number of traps increased as a step function as distance from the point source increased to
228 maintain a reasonable probability of capturing a seed as distance increased. The number of traps
229 was not increased until after 0.75 m to keep the total quantity of traps to a feasible number
230 (Bullock and Clarke 2000).

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

239 Seed traps were placed around one-point source in summer 2013 (Point Source 1) and
240 two point sources in 2014 (Point Sources 2 and 3). Traps were placed around the point source
241 before the siliques began dehiscence and were collected after the vast majority of seeds
242 dispersed. Traps were in the field from July 24th to October 5th and July 12th to August 28th for
243 2013 and 2014, respectively. After the seed traps were collected, the numbers of seeds in each
244 trap were counted in the laboratory at Illinois State University.

245 The total number of seeds dispersed from a point source was estimated by subtracting the
246 number of seeds that were not dispersed from each point source at the end of the experiment,
247 from the estimated total at the beginning. To estimate the initial total number of seeds in a point
248 source, the length of each silique was measured and the number of seeds inside was estimated
249 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

250 silique length in cm (Anderson unpublished data). When seed traps were collected, the siliques
251 remaining in the point source were also collected and the seeds within them were counted in the
252 laboratory.

253 *Estimating Dispersal Kernels*

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

263 For each point source, the $g(r)$ functions were fitted to the seed count data using the
264 following equation:

$$265 \quad n = g(r)AQ \quad \text{eqn. 2}$$

266 where the parameter n was the seed number captured by a trap, $g(r)$ was one of the eight
267 functions evaluated at distance r , A was the area of a seed trap (0.007125 m^2), and Q was the
268 estimated number of seeds within the point source around which the trap was located. Parameter
269 values for the dispersal functions were estimated by non-linear mixed effects modelling, which
270 minimizes the negative log-likelihood value ($-\ln L$) using maximum likelihood (PROC
271 NLMIXED) in SAS[®] software 9.3 (SAS Institute 2012). The default quasi-Newton algorithm
272 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 three point sources.

Dispersal functions were fit to the data using a log-link function and a negative binomial error distribution. A Poisson distribution was also utilized, 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).~~ The selected $g(r)$ was then converted to the $f(r)$ with equation 1. The $f(r)$ was evaluated to determine if it met the requirements of a pdf (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 used to predict the number seeds that would arrive in an area through equation 2. These

296 predictions were then compared to the actual seed counts from the field. The selected $g(r)$
297 function was also compared to the negative exponential from Eschtruth and Battles (2009) by
298 using both functions to predict the change in dispersed seed density as distance increased from a
299 single second-year *A. petiolata* plant. The fecundity of *A. petiolata* plants was set to 156 seeds as
300 this was the fecundity value used in Eschtruth and Battles (2009). The $f(r)$ was analyzed to
301 calculate the median dispersal distance and the distance at which 95% of seed are dispersed by
302 determining the distance at which the $f(r)$ integrated to 0.50 and 0.95, respectively.

303 *Epizoochory Field Experiment*

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

311 Each block contained a mammal inclusion treatment (MIT) and a control. In both
312 treatments, a germination tray filled with potting soil was placed into the ground so it was flush
313 with the ground surface. The MIT was designed to increase mammal activity over germination
314 trays relative to the control. A control replicate consisted of a wood-frame (11 x 61 x 31 cm)
315 completely covered with 1.2 cm² size wire mesh placed over a germination tray. A MIT replicate
316 consisted of a wooden frame (31 x 61 x 31 cm) covered with 2.5 cm mesh poultry fencing placed
317 over a tray. The two 31 by 31 cm ends of the MIT were not covered to allow raccoon-sized or
318 smaller animals to enter. Each frame included a shallow metal pie pan (23 cm diameter) attached

319 to bottom in the center. Only pans in the MIT were filled daily with bait (200 ml equal parts of
320 cracked corn and black oil sunflower seeds) to attract mammals. Within a block, the position of
321 the MIT and control were randomly assigned and were placed one meter apart. All second-year
322 *A. petiolata* plants located within 1.5 m of the block were removed to prevent significant
323 amounts of seed rain from falling into the trays. One motion sensitive camera was placed at each
324 patch to record animal activity around a single block. The MIT and control were both captured
325 within the frame of the camera.

326 The distance between the blocks placed on the north and south sides of the patch and
327 between the blocks on east and west sides was measured. A sampling line was established
328 between the two blocks that were the furthest apart. Ten equally spaced sampling points were
329 established along the line. At each sampling point, a 0.25m² quadrant was placed a random
330 distance between 0 and 100 cm from the transect line and the number of second-year *A. petiolata*
331 plants were counted. This was done to estimate the average density of second-year plants per 1
332 m².

333 Trays were placed in the field during peak seed dispersal. In 2013, the trays were in the
334 field from July 3rd to August 7th. In 2014, at South Breens Woods trays were in field from July
335 2nd to August 8th while at Merwin Nature Preserve trays were out from July 8th to August 8th.
336 After the trays were collected, they were transported to Illinois State University to overwinter
337 outdoors since cold-moist stratification is necessary for seed germination (Baskin and Baskin
338 1992). The trays were moved to a heated greenhouse on Feb 20th in 2014 and Feb 16th in 2015.
339 *Alliaria petiolata* seedlings were counted daily until no new seedlings were observed on two
340 consecutive days, because by this time 95% of the trays had no new seedlings for five
341 consecutive days. Counting was terminated on March 22nd and 12th in 2014 and 2015,

respectively. The majority of seed within the trays are likely to have germinated since 70% of *A. petiolata* seeds germinate the first year. Also, there is no known reason why germination rates would differ between the MIT and control trays.

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. Photos were analyzed using 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. This project was approved by the Illinois State University Institutional Animal Care and Use Committee (IACUC). The IACUC number 14-2013.

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 by 25 cm opening leaving that area of fur uncovered. The

365 two boards were clamped together to secure the pelts. A 9 x 16 cm grid of 144, 2 x 2 cm squares
366 was centered 15 cm above the fur in a horizontal position with the fur side up. In each ~~trial~~^{trial},
367 100 *A. petiolata* seeds were dropped singly through randomly selected squares onto the fur. The
368 pelt and frame were then rotated 180 degrees to an upside down position over a collection box
369 and then immediately turned back to the original position. The number of seeds that remained
370 attached to the fur were counted. Attachment potential was measured as the proportion of seeds
371 that remained attached to the furs after they were rotated. To determine if attachment potential
372 differed between dry and wet fur, furs were misted with 40 ml of water using a plastic spray
373 bottle before the seeds were dropped. ~~Since the seeds were difficult to remove from the wet pelts,~~
374 ~~pelts were dried with a fan after each trial and then the seeds were removed.~~ The moisture of
375 seeds was also manipulated by partially submerging the seeds in water before they were dropped
376 onto the fur.

377 For each fur type (raccoon or deer), 10 replicates trials were used for each of the four
378 treatment combinations, seed dry and fur dry (SD/FD), seed dry and fur wet (SD/FW), seed wet
379 and fur dry (SW/FD), and seed wet and fur wet (SW/FW) for a total of 40 trials per fur type. The
380 raccoon and deer furs were analyzed separately.

381 To test for a significant effect of seed condition, fur condition and their interaction, the
382 data were aligned and rank transformed (ART) since they could not be transformed to meet
383 assumptions of a parametric Analysis of Variance (ANOVA). Data were aligned by removing
384 the marginal means of all other factors from the response variable other than the factor for which
385 the alignment was being applied (Wobbrock *et al.* 2011). For example, to analyze the interaction
386 effect of a two-way factorial, the marginal means of the main effects are removed from each
387 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 ANOVAs 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

Dispersal Kernels

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 and percentage of seeds captured from the point sources was 384 (9.57%), 629 (15.65%), and 682 (14.16%) for Point Sources 1, 2, and 3, respectively. ~~In~~ For all three point sources, the mean number of seeds captured per trap was highest in traps placed at distance 0.25 m, and this number decreased as distance from the point source increased (Table 2). Point Source 1 had the lowest mean number of seeds per trap at distance 0.25 m with 23.4±6.47 seeds per trap and Point Source 2 had the highest with 49.6(±10.51). A small number of seeds ~~were~~ ~~was~~ dispersed 2.25 m with all three

Point Sources averaging less than one seed per trap. Even fewer seeds were dispersed 3.25 m with all point sources averaging below 0.5 seeds per trap (Table 2).

The AIC scores of the eight $g(r)$ dispersal functions 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. Because the Weibull ~~did not meet~~ ~~not meeting~~ the pdf requirement, the lognormal function was selected next 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. However, 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. This prediction was in direct contradiction with field observations that many seeds fall directly below the parent plant, which should result in the density probability being greater than zero at distance zero. Because of this unrealistic prediction, the lognormal function was not used for further analysis.

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. 2). This result is more in agreement with field observations and is different than the lognormal. Beyond 0.25 m, the $g(r)$'s probability densities of the 2Dt rapidly declined as distance increased to one meter. As the distance increased beyond one meter, the probability density asymptotically approached zero.

The 2Dt $g(r)$ function was placed into equation 2 to predict the seed counts per trap for each of the point sources separately. 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 less than one seed per trap is predicted. The predicted seed count per trap continues to decrease beyond 1.30 m

~~meters~~ *[use of 'meters' and 'm' is inconsistent; standardize.]* asymptotically approaching zero (Fig. 3).

The predicted change in dispersed seed density from a single second-year plant as estimated by ~~of~~ the 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 2Dt function ~~beginning~~ at 0.5 m and beyond from the point source (Fig. 4). 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 2Dt $g(r)$ function. *[Drop this sentence; it's redundant, and calling this an 'over-estimate' implies an a priori judgment that the 2Dt function is correct, when the neg exp could, in principle, actually be the more accurate at distances > 0.50 m].*

The corresponding $f(r)$ of the 2Dt function has 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 1. The probability density of the 2Dt function rapidly increases between 0 and 0.25 m and peaks at 0.35 m, meaning seeds have the highest probability of dispersing this distance (Fig. 5). The probability density then steadily declines to around 1.20 m ~~and where beyond that distance it~~ asymptotically approaches zero ~~beyond that distance~~. The median, mean, and the distance at which 95% of seeds were dispersed within are 0.47, 0.53 and 1.14 m.

The parameter values for the 2Dt function were based on the pooled data of the three replicate plots (Table 3). SAS approximates the standard errors, P-values are for $\alpha < 0.05$ and hypothesis of parameter=0. Variation in seed counts within traps was not significantly different among the three point sources as the parameter u was not significantly different than zero. The

parameter k was less than one, which indicates that there was a high amount of variation around the expected seed trap values (Clark et al 2005). The high variation is apparent when ~~comparing~~ observing the predicted seed counts per trap of the dispersal functions to the actual seed counts from the traps in the field (Fig. 3). 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~~ [these are actual min-max values?] 117 seeds per trap, and ~~at the 0.5 m distance they varied~~ from 2 to 59 at 0.5 m distance.

Epizoochory Field Experiment

The bait placed in the MIT was removed daily for ~~most~~ the vast majority of pie pans in both years, indicating animals were visiting the treatments with a high frequency. 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 controls. Raccoons accounted for the ~~vast~~ majority of animal visits and ~~it was~~ were the only animal recorded at all seven *A. petiolata* patches (Table 4). Raccoons entered the MIT wood frames and stood directly over the germination trays while feeding. Turkeys (*Meleagris gallopavo*) were the second most common animal visitor, but they were only recorded in the year 2014 and only at the South Breen Woods. 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 by inserting only their head~~ down outside of the frame edge 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 in significantly more ($F_{1,27}=129.5$, $p<0.0001$) *A. petiolata* seedlings than in control trays, with average. ~~The difference in *A. petiolata* seedling counts between treatments was quite large with~~

the MIT counts more than averaging over one order of magnitude greater more than for the control trays (Fig. 6).

The seven *A. petiolata* patches used in this experiment varied in patch size and in density of second-year plants (Table 5). 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 both). The variation due to block was estimated to be zero; therefore, SAS PROC MIXED did not test for significance.

Seed Attachment

For the deer pelt treatment, the main effects of fur ($F_{1,39}=56.44, P<0.0001$) and seed ($F_{1,39}=110.3, P<0.0001$) conditions, and their interaction ($F_{1,39}=59.8, P<0.0001$) significantly affected attachment potential. Fur ($F_{1,39}=3920.4, P<0.0001$) and seed conditions ($F_{1,39}=100.39, P<0.0001$), 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. 7a). 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. 7b). 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 for SW/FW treatments, despite having~~
high attachment potential values, ~~were due but this is because both wet fur and wet seeds had to~~
strong positive effects on attachment potential ~~of both wet fur and wet seeds, with no .However,~~
~~when these two effects were combined, it did not result in an~~ increase in attachment potential ~~in~~
~~the combined treatment. 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. 8). The difference
in retention potential between wet and dry fur was large for both pelt types. ~~For raccoon fur,~~
~~The retention potential for the dry raccoon fur ranged from values ranged from 2-5% for dry fur~~
compared to ~~the wet fur which ranged from 94-100% for wet fur; for deer fur, values. The~~
~~retention potential for dry deer fur ranged from 1-6% for dry fur and and it ranged from 81-98%~~
for wet ~~fur~~. 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

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), although ~~their estimates from prior studies~~ estimates that most seeds fell
within 1-2 m of the parent plants are consistent with our results. The mean and median seed

dispersal distances predicted by the 2Dt function were about 0.50 m, which is substantially less than the 1.28m (range 1.03-1.63m) predicted by Biswas and Wagner (2015) who used an experimental design similar to ours. However, the first seed traps in ~~his-that~~ study were placed 0.50 m from the point seed source which may have resulted in the majority of dispersed seeds being missed as our results indicate peak seed dispersal occurred at 0.35. This likely caused the average dispersal to be overestimated.

The 2Dt function predicted that the distance at which 95% of *A. petiolata* seeds are dispersed is about 1.14 m, which is substantially 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), ~~suggesting an~~ ~~Our results suggest that the value of *b* is an imprecise estimate, and as a result, the negative exponential function is~~ overestimation ~~ngof~~ seed dispersal distances ~~in those studies~~. 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 2Dt function (Fig. 4). The negative exponential ~~overestimates 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.

With only 5% of *A. petiolata* seeds being dispersed over 1.14 m (Fig. 3), *A. petiolata* is similar to most plant species in that the vast majority of seeds are dispersed within a short distance from 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 to the spread of a species across the landscape 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). Our results indicate the epizoochory is likely one mechanism by which seeds can be dispersed greater distances ~~are dispersed beyond 1.14 m.~~

This study is the first to provide experimental evidence that epizoochory through woodland animals is a potential seed dispersal mechanism of *A. petiolata*. The MIT germination trays had significantly more animal visits than the control trays (Table 4) which resulted in the MIT trays having significantly more *A. petiolata* seedlings (Fig. 6). ~~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. [I'd suggest dropping or modifying this sentence, since the lower direct contact by other animals could be entirely an artifact of the experimental design/cage design.]~~ The laboratory studies provide evidence that seeds can adhere to raccoon and deer fur sufficiently for dispersal ~~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. 7 and 8). 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). Since attachment and retention potential increased when seeds or fur were wet (Fig. 7 and 8) it is likely wet environmental conditions, such as rainfall or heavy dew, increase *A. petiolata* epizoochory potential.

Alliaria petiolata seeds that are retained within deer and raccoon fur have the potential to be dispersed several kilometers by these animals. 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), particularly with larger home ranges. Since the retention potential of *A. petiolata* seeds significantly increased when either seeds or fur were wet, this retention pattern could result in increased retention time and dispersal distances. Therefore, *A. petiolata* seeds may be dispersed up to several miles by deer and raccoon as these mammals have large home ranges. [repetitive.] 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 Fritz 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 exhibit are still capable of epizoochory-dispersal, albeit at a lower proportion of total seed production compared to plant species with specific adaptations (Fisher *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 [implication clear enough; don't need to spell it out...]. (Will and Tackenberg 2008; Courvreur *et al.* 2008). Additionally, autogamy in *A. petiolata* can allow establishment of new populations from a small number of dispersed seeds, 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, epizoochory may be an important mechanism for the spread of *A. petiolata* across the landscape, accounting for rates of expansion greater than as it can explain how *A. petiolata* spreads much faster than

618 the predicted rate of less than one meter per year (Nuzzo 1999). Epizoochory may also contribute
619 to *A. petiolata*'s invasion success as it may increase the probability that seeds are deposited on
620 favorable microsites within woodlands (Nathan and Muller-Landau 2000).

621 Endozoochory (seed dispersal in animal guts) is another common seed dispersal
622 mechanism, but it is highly unlikely that that it is a dispersal mechanism of *A. petiolata*. *Alliaria*
623 *petiolata* experiences very little herbivory (Evans and Landis 2007, Riper *et al.* 2010) due to
624 production of toxins in plant tissues such as cyanide and glucosinolates (Barto *et al.* 2010,
625 Cipollini and Barto 2007). Hydrochory (seed dispersal through water) has been suggested as a
626 seed dispersal mechanism of *A. petiolata* due to it being prevalent in river bottom and floodplain
627 areas (Nuzzo 1999, Meekins and McCarthy 2001). While hydrochory may occur, this does not
628 explain how *A. petiolata* spreads into upland areas (Burls and McClaugherty 2008), spreads up
629 stream (Nuzzo 1993), or how it disperses locally across the landscape (Eschtruth and Battles
630 2009). Hydrochory also does not explain the *A. petiolata* seedling differences between the MIT
631 and control germination trays, because the two treatments did not experience any differences in
632 the flow of water from the ground surface into the trays.

633 Causes for increased attachment and ~~The cause for why~~ retention potential when seeds or
634 fur are wet are unclear, and also attachment potential, increase when the seed or fur are wet is
635 unclear. Some plant species produce seed coat mucilage when wet ~~and this mucilage can have a~~
636 ~~variety of functions with one being increased~~ increasing epizoochory dispersal ['epizoochory
637 dispersal' is redundant!] (Yang *et al.* 2012). When *A. petiolata* seeds were observed under a
638 light microscope, they did not appear to produce any mucilage when wet. Another possibility is
639 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 as a dispersal agent for *A. petiolata*.

Another topic that needs further clarification is the role genetic and environmental variation plays in *A. petiolata* seed dispersal. Byers and Quinn (1991) found that certain *A. petiolata* traits, such as seed mass, differed among studied habitats. Susko and Lovett-Doust (2000) reported that *A. petiolata* *[is this variability in particular trait(s)?]* was highly variable among and within populations. It is unknown how the variability in such traits as seed mass may ~~affect~~ seed dispersal distances. Environmental effects on *A. petiolata* also need to be studied as other studies have found that such factors as habitat type ~~affect~~ dispersal distances (Fontúrbel *et al.* 2017). It will be important to study these factors to further improve seed dispersal estimates of *A. petiolata*.

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