



Random walk modeling of adult *Leuctra ferruginea* (stonefly) dispersal



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ABSTRACT

Aquatic insects of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) are commonly used as indicators of freshwater quality. Recolonization of restored waterways by these pollution intolerant insects is frequently employed to measure the success of stream restoration efforts. Post restoration monitoring programs based on recolonization by EPT indicator species are typically generalized with little consideration for local conditions. Within Philadelphia urban development has resulted in a loss of unimpaired headwater streams that might serve as refugia of EPT colonists to replenish downstream populations through passive drift of larvae and ova. In this urban setting, recolonization may depend largely on overland flight by adults from other systems.

In an attempt to predict the likelihood of overland dispersal by adult EPT within Philadelphia, PA, USA, a one year field study was conducted at the Schuylkill Center for Environmental Education (SCEE) in Northwest Philadelphia to obtain data on local EPT taxa and dispersal behavior. Adult EPT specimens belonging to 15 species were collected using sticky traps extending laterally from Meig's Run, a 1st order tributary to the Schuylkill River. *Leuctra ferruginea* (Plecoptera: Leuctridae) was selected as the study species.

A random walk model was developed and calibrated to field observations to predict long distance dispersal probability. An individual-based Lévy flight random walk model provided the best fit for field observations from Meig's Run, as well as supporting observations and theory proposed in existing literature.

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1. Introduction

Biomonitoring is the practice of using measureable aspects of an ecosystem to assess the overall water quality and health of the ecosystem. Monitoring aquatic organisms, as opposed to chemical composition of the water, can provide a more thorough temporal and spatial view of water quality. The presence or absence of an indicator species, or a species intolerant of poor water quality, can simplify a water quality monitoring program. The presence of biological indicator species can provide evidence that water quality has been sustained over a period of time throughout the spatial domain of the species. Chemical sampling, in contrast, only provides a picture of water quality at the time and location of sampling (Barbour et al., 1999).

Aquatic insects of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) are generally sensitive to aquatic pollution (PADEP, 2012). Rapid bioassessment protocols aim to characterize the health of an aquatic ecosystem by sampling the benthic assemblage. The presence or absence of EPT insects within samples is a primary component of several common indices of water quality (Barbour et al., 1999).

Many stream restoration projects are planned around the "Field of Dreams" hypothesis ("If you build it they will come") (Palmer et al.,

1997). The premise of this theory is that restoring the physical and chemical assemblage of an impaired water body will lead to a restoration of the natural biotic composition. Hilderbrand et al. (2005) note that stream and wetland restoration projects that focus primarily on physical restoration often include little consideration for biological processes and rely heavily on self-assembling ecosystems. Recolonization of a restored water body by aquatic macroinvertebrates is assumed to occur naturally within a fairly short time frame. Engineering projects to restore waterways are typically subject to arbitrarily defined grant and permit timelines for demonstrating an improvement in aquatic life use. One possible template for post restoration monitoring is the EPA established five year monitoring program for wetlands, with considerations for additional years if the ecosystem has not yet reached steady state (EPA, 2013).

Within Philadelphia, the majority of streams and rivers are considered impaired for aquatic life use, generally lacking sensitive EPT insects when assessed with rapid bioassessment techniques (PADEP, 2012). Philadelphia's streams have had a large overall proportion of small tributaries filled in and piped to sewers in order to facilitate urban development. These streams thus lack unimpaired headwater streams that would tend to serve as refugia and sources of colonists to replenish downstream populations through passive drift. In these cases, recolonization may depend largely on overland dispersal by adults from other systems (PWD, 2004).

Overland dispersal of adult aquatic insects as a means of recolonization has received limited attention compared with dispersal through

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downstream drift of the aquatic stages. A review of existing literature that shows dispersal by adults has been studied, though typically at undisturbed natural streams over limited distances (Finn and Poff, 2008; Griffith et al., 1998; Jackson and Resh, 1989; Jones and Resh, 1988; Macneale et al., 2005; Petersen et al., 1999, 2004; Winterbourn and Crowe, 2001).

Available research, while setting a firm theoretical framework for future studies, provides little practical guidance for estimating the probability of successful inter-basin transfer of EPT ova. When predicting dispersal probabilities, local variables must be considered including: local EPT taxa and abundances, land use and the degree of habitat segmentation.

A predictive model provides a theoretical framework to allow extrapolations beyond the boundaries of a given study. Once validated, a model for freshwater macroinvertebrate dispersal can be used to refine expectations for recolonization by EPT. This research discusses numerical models for predicting insect flight. Several random walk models are fit to field observations to make inferences about adult macroinvertebrate behavior, and to set a foundation for prediction of long distance dispersal probability.

2. Methodology

2.1. Field observations

A one year field study of adult EPT dispersal was conducted from April 15, 2012 through April 14, 2013 at the Schuylkill Center for Environmental Education in Philadelphia, PA, USA. The study site was adjacent to Meig's Run, a 1st order tributary to the Schuylkill River. Meigs' Run has a drainage area of 0.7 km². The average channel slope along the tributary is 4%. Stream top width varies from 1.5 to 3 m. Meig's Run is approximately linear with few meanders (sinuosity index = 1.11). The land was farmed until the mid 1960s when the property was designated for educational use and as a nature preserve (SCEE, 2012). The study watershed is among the least disturbed watersheds within Philadelphia. Each drainage basin contains minimal development at less than 5% gross impervious cover. The upper 10% of the drainage basin collects overland runoff from a detached single family home residential area. The lower 90% has reforested though the understory is heavily grazed by deer.

Trapping methods used in this study were similar to those described by Jackson and Resh (1989) and Petersen et al. (1999). At 2 separate trapping locations, 3 square 0.36 m² sticky traps were placed on wooden posts along a lateral transect from Meig's Run at distances of 5.8 m, 15 m and 30.2 m from the stream centerline at location 1 and 7.6 m, 14 m and 26.8 m at location 2. The midpoint of each trap was set at a height of 1.5 m above ground. Each trap was constructed of plywood that had been covered in removable clear plastic sheets. The plastic sheets were sprayed with Tanglefoot Tangle Trap Sticky Coating (Contech, Victoria, BC) to trap flying insects. Traps were visited every two weeks to collect EPT specimens. Specimens were removed from the traps by soaking the plastic in Winsor & Newton Oil & Alkyd Solvents English distilled turpentine. Specimens collected were sorted into glass vials according to collection date, trap and species. Specimens were preserved in a solution of 95% ethyl alcohol. Funding for field and lab supplies was provided by the Philadelphia Water Department (PWD).

Identification of species and sex for EPT insects was carried out using Usinger (1956), Hitchcock (1973), Bauman (1975) and Merritt and Cummins (1996). Identification was carried out with a Lomo M6C-10 stereoscopic dissecting microscope. Identification photographs were taken directly through the ocular tube with an Olympus Stylus 850SW digital camera. *Leuctra* females within the region were differentiated with Hitchcock (1973) and comparison to type specimens held in the Entomology Type Collection of the Academy of Natural Sciences of Drexel University, Philadelphia, PA (ANS, 2013).

To supplement visual identification, DNA barcoding of the mitochondrial cytochrome c oxidase subunit I gene of 100 specimens was performed at the University of Guelph Canadian Centre for DNA Barcoding (Project Code: SCAMI) (BOLD, 2013). Results of DNA barcoding confirmed visual identifications. Funding for DNA barcoding was provided through a research award from the University of Pennsylvania. Voucher specimens for each taxon have been submitted to the Entomology Type Collection of The Academy of Natural Sciences of Drexel University, Philadelphia, PA (ANS, 2013).

Leuctra ferruginea (Plecoptera: Leuctridae) was the most numerically abundant taxon collected over the trapping period. Review of field observations suggests that *L. ferruginea* exhibits some dispersal behavior, being captured commonly even at the furthest traps. Based on these initial field observations, *L. ferruginea* were selected for further study as a potential higher frequency dispersing EPT insect, and therefore a more probable colonist of restored waterways.

2.2. Review of existing models and data to describe insect flight

Two theoretical models for dispersal of adult *Leuctra* spp. have been proposed. The model of Macneale et al. (2005) suggests that dispersal is primarily upstream within the stream corridor with occasional unpredictable long distance lateral dispersal. Petersen et al. (2004) similarly propose a theoretical model suggesting two possible outcomes for a female stonefly, overland dispersal or a return to the stream of emergence. Both models are somewhat unsatisfying in that they propose that *Leuctra* spp. behavior is to remain within the stream corridor, yet they allude to infrequent long distance dispersal events with no attempt to explain or quantify this rare behavior.

Quantitative studies of *L. ferruginea* flight corroborate field observations obtained through this study. Through a mark and recapture experiment, Macneale et al. (2005) tracked the flight behavior of *L. ferruginea*. Recapture of marked females demonstrated the capacity for overland dispersal of distances up to 560 m and 640 m along the stream corridor.

There is scant published information about short duration *L. ferruginea* flight behavior. Macneale et al. (2005) remark that while *L. ferruginea* are considered poor flyer, they were observed to fly in bouts with typical lengths of up to several meters. These qualitative observations are similar to observations the authors made while collecting stoneflies within the Schuylkill Center. Leuctrids were often observed flying a few meters in several minutes, but never a sustained continuous flight in a consistent direction. Following a bout of flight, the stoneflies landed on nearby trees or sticky traps more commonly than on the ground (J. Knighton, personal observation, 2012).

A variety of numerical models have been proposed to simulate the dispersal of insects (Freeman, 1977; Mayer et al., 1999; Petersen et al., 2004; Petrovskii et al., 2011b). Existing models range in complexity, data requirements, computational demand and the underlying theory describing insect movement.

A regression analysis of insect trap data versus distance (Griffith et al., 1998; Jackson and Resh, 1989; Petersen et al., 2004) is a simplistic statistical model which can be useful tool in testing the hypothesis that stonefly density decreases with distance from the stream. While regression against distance is a valuable tool that is simple to implement, it over simplifies the phenomena as extrapolation can yield results with no physical basis.

Freeman (1977) proposed a mathematical model to explain the dispersal patterns of flying insects. The basic theory behind this model is that given a single point of emergence, insect density will decrease with distance from this point. Freeman acknowledges that there is a random component to insect movement; however the proposed model is deterministic in nature. This model was originally used to fit data from a mark and recapture experiment with cabbage flies. Similarly, this model is useful only for interpolation between traps and yields physically impossible results when extrapolating.

Mayer et al. (1999) propose a continuous population density function based on Cauchy dispersal over a circular area to explain the dispersal patterns. Estimates of the lifespan of the study insect and average daily flight distances are required. This model was originally used to model a 1967 screwworm outbreak in Texas. The main limitation of Mayer's model is that it solves for proportion of the population instead of number of dispersing insects. Validation of the model requires additional data or assumptions about relationships between trap counts and density.

The random walk approach (Petrovskii et al., 2011b) is stochastic in nature, which allows movement parameters to be defined as random variables. As the flight of insects is generally considered to be a highly random process (Freeman, 1977; Mayer et al., 1999; Petrovskii et al., 2011b) this approach provides more flexibility in describing stonefly flight. In addition, it allows for inferences on population density from trap counts. As such, the random walk approach meets the fundamental criteria for this research.

2.3. Proposed modifications for individual based random walk modeling

The individual based random walk model developed for this study is based on the model described by Petrovskii et al. (2011b). The model is of a generalized form, originally designed to simulate the dispersal of aphids, a crawling terrestrial insect. While the basic framework of this model is maintained in this study, several modifications are proposed to better approximate the phenomenon of stonefly emergence and dispersal.

The timing of emergence is assumed to be completely synchronous. Random walks for all individuals begin at time equal to 0. While emergence of each stonefly species trapped was observed over a period of weeks during 2012, interactions between stoneflies are not being simulated, and it is therefore not required that the temporal variation of emergence be accounted for. The primary question to be asked in this research is how many years before dispersal will occur, therefore differences in emergence times on the order of weeks are considered inconsequential.

The lifespan of all dispersing stoneflies is assumed to be identical. Research by Petersen (2002) suggests that the life span of *Leuctra* spp. may be best represented as a continuous probability density function. Though a more accurate representation of lifespan would improve model estimates, a lack of existing data on the study species prevents variation in lifespan from being described as a random variable. A constant average lifespan is proposed as a substitute for an experimentally defined probability distribution. For this set of simulations, random walks end at time equal to estimated average lifespan of 900 h as the average of lifespan of *Leuctra* spp. proposed by Petersen (2002).

The typical mark and recapture simplifying assumption employed by Petrovskii et al. (2011a) that all insects begin at a central location are somewhat valid for stonefly dispersal in nature. The starting location for all stoneflies is assumed to be centered on a riffle. While riffles along the Schuylkill Center are roughly 2.3 m², the variation in potential emergence location is small compared to the entire simulated spatial domain. The simplifying assumption that all stoneflies within of a given riffle emerge from the same point is presumed to be valid.

Rather than accounting for all stoneflies along a given stream, the model is simplified to simulate three riffles within the vicinity of the sticky traps. Migration along the stream corridor creates a flux of stoneflies through the imaginary model boundaries. To implicitly account for migration along the stream within the simulation a reflective border is placed on either side of the study domain extending laterally from the stream (spatial domain demonstrated in Fig. 1a–d). The use of reflective boundaries assumes that for every stonefly leaving the study area, there will be approximately one stonefly entering the study area originating from an adjacent riffle.

Traps are approximated as discrete spherical areas within the spatial domain. Simulated insects are removed from the study area if they enter

the space defined as the trap as recommended by Petrovskii et al. (2011b). In reality, the trapping of insects may create a measureable local perturbation in stonefly density (Freeman, 1977; Petrovskii et al., 2011b) allowing the influx of stoneflies from adjacent riffles to outweigh the numbers leaving the study area. In order to counteract the numerical artifacts arising from this local perturbation, 3 riffles are simulated with reflective boundaries on either side of the outer riffles. Inclusion of more than 3 riffles significantly increases computational demand of each simulation while not providing a marked improvement in results.

Height of aquatic insect flight through a forest was studied by Jackson and Resh (1989). Traps hung at 2, 5 and 8 m above ground showed little preference among adult EPT insects for a specific height. Based on these observations, flight elevation preference is assumed to be negligible. Research suggests that stoneflies are commonly associated with tree and bankside vegetation (Harrison et al., 2000; Hitchcock, 1973; Sweeney, 1993), therefore the upper elevation of the shrub layer is used to define an artificial vertical reflective boundary at 6 m.

In one of the earliest studies of adult stonefly dispersal, Ulfstrand (1969) proposed that stoneflies may have the ability to cover large distances through wind aided dispersal. Research by Madsen et al. (1973) and Winterbourn and Crowe (2001) suggests that flight direction of EPT insects may not be a function of wind direction. In the study by Madsen et al. (1973) EPT dispersal was observed against wind. Briers et al. (2003) discuss the flight activity of stoneflies in relation to meteorological conditions such as air temperature and wind speed. Their findings suggest that flight activity is negatively correlated with wind speed. Though at present there is a consensus among authors that wind must affect dispersal to some degree there is little evidence available to support the claim. If observed dispersal distances are proven infeasible to explain field observations on stonefly dispersal, it may be more useful to study the joint probability of the co-occurrence of stonefly emergence and significant weather events.

Jackson and Resh (1989) proposed that environmental variables such as vegetation and slope of the surrounding land may affect lateral EPT dispersal. The results of the field observations on stonefly dispersal at Meig's Run did not show differences in dispersal between locations 1 and 2, therefore no conclusions can be drawn regarding any potential environmental effects. Similarly, Petersen et al. (2004) and Collier and Smith (1995) studied dispersal of stoneflies across a variety of non-urban land types and found no significant correlation between lateral dispersal and environment.

The effects of urban environments on EPT dispersal have received attention; however existing data is primarily qualitative. Artificial lighting and reflective surfaces have been known to attract adult aquatic macroinvertebrates and cue oviposition (Horvath et al., 2009; Kriska et al., 2009; Malik et al., 2008; White and Shardlow, 2011). As the field study was only conducted within a wooded area, the effects of urban development on stonefly dispersal cannot be assessed. As a simplifying assumption the spatial environment is considered isotropic through all scenarios, however it is noted that natural as well as anthropogenic environmental barriers to dispersal exist.

2.4. Mechanisms for random walks

The flight behavior of individual stoneflies is a largely unstudied subject. This uncertainty resulted in development of several hypotheses for flight behavior, and subsequently several different models. Three models incorporating Brownian motion, Brownian motion introducing variation among individuals and Lévy flight behavior were evaluated against observed trap counts.

Deviating from the solution technique proposed by Petrovskii et al. (2011b), bout direction and step length are solved independently. The change is introduced only for conceptual simplicity as it yields identical results. Direction is assumed to be continuously uniformly distributed in three dimensions, which suggests that the stoneflies exist in an isotropic

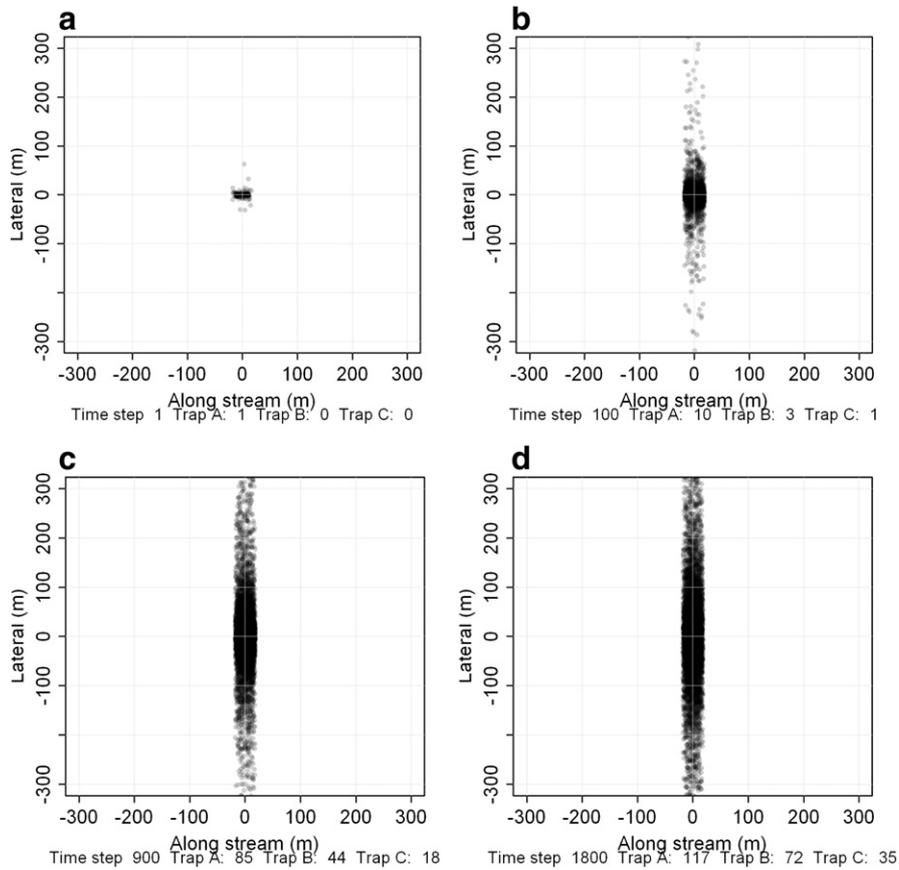


Fig. 1. Top down view of random walk spatial domain for time steps $t =$ a) 1, b) 100, c) 900 and d) 1800 h.

environment and show no interactions among individuals. For each time step, three continuous random variables are sampled from -1 to 1 to create vectors in the x , y and z directions. The unit vector defined by the three random variables is then solved and applied to the step length to yield a random walk in three dimensions. All models discussed were developed within R x64 2.15.0 (R Core Team, 2012).

2.4.1. Brownian motion

A simplistic starting assumption for individual based modeling is that stonefly movement follows a Brownian random walk. Random walks consisting of Brownian motion have been widely proposed as valid models for simulating animal movements (Bovet and Benhamou, 1988; Crumpacker and James, 1973; Kareiva and Sigesada, 1983; Okubo and Levin, 2001; Petrovskii et al., 2011a,b; Turchin, 1989, 1991). An individual exemplifying a Brownian random walk suggests non-specialized behavior with respect to motion (Reynolds and Rhodes, 2009).

Field observations by Macneale et al. (2005) suggest that *L. ferruginea* typically fly in discrete bouts of up to several meters. Research by Marden (2007) estimated maximum flight speeds of various adult stonefly species in the range of 60 to 70 cm/s. These observations provide some basic data for developing a distribution for stonefly flight bout length. Bout length (Δx) at each time step is defined as a random variable sampled from a normal distribution with mean, $\mu = 0$ (Eq. (1)). Direction is assumed to be continuously uniformly distributed, which suggests that the stoneflies exist in an isotropic environment and show no interactions among individuals.

$$\phi = \frac{1}{\delta\sqrt{2\pi}} \exp\left[-\frac{\Delta x^2}{2\delta^2}\right]. \quad 1$$

where,

ϕ – step length probability density function of an individual

δ – standard deviation

Δx – step length for duration Δt

Δt – time step

The model parameter δ , or standard deviation of the step length distribution, represents the sole calibration parameter describing dispersal capabilities of the stonefly. The parameter n directly accounts for number of dispersing insects per riffle. Each parameter was adjusted for each data set until the G-test statistic was minimized. The maximum estimated 30 minute flight distance was calculated as 1262 m based on data from Marden (2007). Step length values exceeding this estimated maximum were recalculated.

2.4.2. Lévy flight

Lévy flights are characterized by longer periods of short random movements interspersed with shorter periods of large movements in a consistent direction. A Lévy flight can be defined as any movement where the step length is defined by a heavy tailed distribution. Similar to the above assumption of Brownian motion, Lévy flight produces primarily short bouts of up to several meters, which is in agreement with field observations by Macneale et al. (2005).

Lévy flights are a commonly observed as a technique employed by animals in nature to optimize search efficiency when resources are limited (Cole, 1995; Humphries et al., 2011; Reynolds and Rhodes, 2009; Viswanathan and Raposo, 2008; Walters et al., 2006). Observation of Lévy flights is considered a significant finding as it indicates that movement behavior is an evolved trait specific to a particular taxon rather than non-specialized movement (Reynolds and Rhodes, 2009). Though Lévy flights are typically observed in more advanced animals, they have

been observed within the insect orders Diptera (Cole, 1995) and Hymenoptera (Reynolds and Rhodes, 2009).

Adult stoneflies search for food, water, resting locations, mating opportunities or in the case of gravid females locating a stream for oviposition (Hitchcock, 1973). It has been observed that some stoneflies rely on chance encounters for mating. Coleman and Hynes (1970) observed that males of *Allocaupnia pygmaea* could only recognize mates within a 15 cm radius. As Lévy flights are commonly used to increase search efficiency when resources are scarce (Humphries et al., 2011), it is feasible that stoneflies evolved Lévy flight behavior to increase reproductive success. For the purposes of this model a Cauchy distribution is used to generate the step length of the Lévy flight (Eq. (2)). As above, direction and step length are solved independently. Direction is assumed to be continuously uniformly distributed, which suggests that the stoneflies exist in an isotropic environment and show no interactions among individuals.

$$\phi = \frac{1}{\pi\alpha \left[1 + \left(\frac{\Delta x}{\alpha}\right)^2 \right]} \quad 2$$

where,

- ϕ – step length probability density function of an individual
- α – shape parameter
- Δx – step length for duration Δt
- Δt – time step

The model parameter α , or shape parameter of the Cauchy step length distribution, represents the sole calibration parameter describing dispersal capabilities of the stonefly taxon. As above, n directly accounts for number of dispersing insects per riffle. As described above, step length values generated exceeding 1262 m were recalculated.

2.4.3. Brownian motion introducing variation among individuals

A population wide heavy tailed step length distribution can be demonstrated through Lévy flight of individuals as demonstrated above. An alternate explanation is that individuals follow Brownian motion and some variation among individuals exists. The random path of an individual can remain thin tailed as found in Brownian motion however introducing variation among individuals produces a population demonstrating heavy tailed dispersal (Petrovskii et al., 2008, 2011b).

Morphological differences such as wing length have been correlated positively with dispersal capability of stoneflies (Malmqvist, 2000). Qualitative observations made during identification of specimens collected during this study suggest that there is some degree of physical variation among stoneflies of the same species with respect to wing length and body size. It is feasible that the underlying mechanisms for dispersal are identical; however the step length is increased for individuals that naturally possess greater dispersal capabilities.

Variations are introduced among individuals by assigning the standard deviation of the individuals' step length distribution as a random variable. The step length standard deviation is defined as the absolute value of a random number sampled from a normal distribution as one of several cases proposed in Petrovskii et al. (2008). The mean and standard deviation of the distribution defining variation among individuals are treated as additional calibration parameters.

3. Results

3.1. Results of field observations

Through the field study, 859 EPT specimens were trapped belonging to 15 taxa. Stoneflies (Plecoptera) dominated trap counts of all EPT with 831 stonefly specimens collected belonging to 7 taxa, 788 of which species and sex could be determined (Table 1).

Table 1
EPT taxa trapped at SCEE, Philadelphia PA.

Order	Family	Genus	Species	n	Pollution tolerance ^a
Ephemeroptera	Baetidae	<i>Baetis</i>	sp.	2	6
Ephemeroptera	Heptageniidae	<i>Maccaffertium</i>	<i>pubidum</i>	1	3
Ephemeroptera	Leptophlebiidae	<i>Paraleptophlebia</i>	<i>debilis</i>	4	1
Ephemeroptera	Leptophlebiidae	<i>Paraleptophlebia</i>	<i>guttata</i>	4	1
Plecoptera	Capniidae	<i>Allocaupnia</i>	<i>recta</i>	141	3
Plecoptera	Leuctridae	<i>Leuctra</i>	<i>ferruginea</i>	512	0
Plecoptera	Leuctridae	<i>Leuctra</i>	<i>variabilis</i>	23	0
Plecoptera	Nemouridae	<i>Amphinemura</i>	<i>nigrita</i>	50	3
Plecoptera	Nemouridae	<i>Prostoia</i>	<i>similis</i>	1	2
Plecoptera	Nemouridae	<i>Soyedina</i>	<i>vallicularia</i>	43	0
Plecoptera	Perlodidae	<i>Isoperla</i>	<i>holochlora</i>	18	2
Trichoptera	Hydropsychidae	<i>Diplectrona</i>	<i>modesta</i>	2	0
Trichoptera	Philopotamidae	<i>Dolophilodes</i>	<i>distinctus</i>	6	0
Trichoptera	Rhyacophiliidae	<i>Rhyacophila</i>	<i>invaria</i>	3	1
Trichoptera	Uenoidae	<i>Neophylax</i>	<i>mitchelli</i>	3	3

^a PA Department of Environmental Protection Genus Level Pollution Tolerance (PADEP, 2012).

In North America, *L. ferruginea* displays indeterminate voltinism (univoltine to semivoltine) depending on stream temperature (Grubbs et al., 2006). Over the summer of 2012, *L. ferruginea* were captured within the Schuylkill Center for Environmental Education over two distinct emergence periods. The 1st emergence occurred from May through July followed by a 2nd fall emergence spanning mid-August through early December. The second emergence period appeared to be somewhat less synchronized than the first, occurring over roughly twice the duration (Fig. 2). It is assumed that two separate cohorts of *L. ferruginea* emerged during the observation period.

Trap counts of *L. ferruginea* females (Fig. 3) from the field study were used for development and evaluation of several models to describe adult stonefly dispersal. Successful inter-basin transfer of ova is dependent on overland dispersal by gravid females. While inter basin dispersal by males may be important for introducing genetic variation, recolonization of restored streams will not occur through male dispersal. A total of 4 validation data sets were generated through trapping 2 separate cohorts of *L. ferruginea* females at 2 trapping locations.

3.2. Brownian motion model calibration

A calibration of the 4 data sets of *L. ferruginea* female trap counts yields a final average calibration parameter of $\delta = 3.7$ (parameter value standard deviation = 1.59) for this taxon. Population density, n , is expected to vary by location and cohort. The comparison to observed trap counts of *L. ferruginea* females suggests that Brownian motion within an isotropic environment may be a sufficient explanation for stonefly flight behavior. Statistically significant calibration results

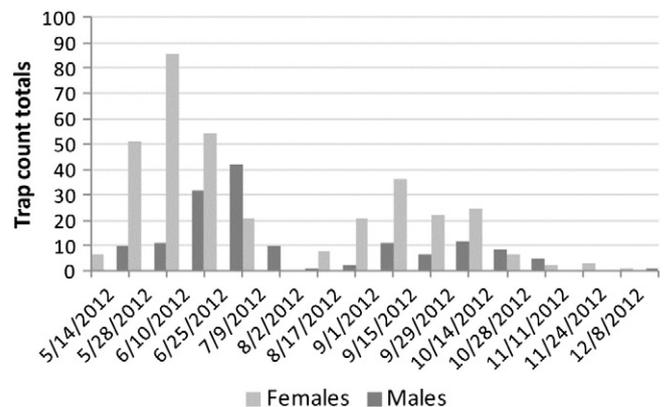


Fig. 2. Emergence pattern of *L. ferruginea* (Totals of all trap counts).

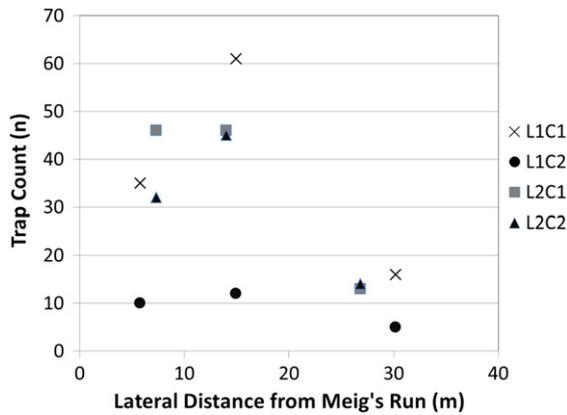


Fig. 3. Trap counts of *L. ferruginea* females for Location (L) and Cohort (C).

were obtained for 3 of 4 calibration datasets (G-test; H0: model is a valid predictor of trap counts; p value ≥ 0.05) (Table 2).

3.3. Lévy flight model calibration

A calibration of the 4 data sets of *L. ferruginea* female trap counts yields a final averaged calibration parameter of $\alpha = 0.313$ (parameter value standard deviation = 0.043) for this taxon. Population density, n , is expected to vary by location and cohort. The comparison to observed trap counts of *L. ferruginea* females suggests that Levy flight within an isotropic environment may be a possible explanation for stonefly flight behavior. Calibration to all validation datasets produced statistically significant results (G-test; H0: model is a valid predictor of trap counts; p value ≥ 0.05) (Table 3).

3.4. Brownian motion introducing variation among individuals

As with the other proposed models, a series of calibrations was performed against field observations employing the G-test statistic as the objective function. Results of these calibration attempts showed that while statistically significant results could be reached with the proposed model, parameter values were not converging among repeat calibrations. This result suggests that many local optima exist for the proposed model when validated against the field observations.

Given that the problem contains many local optima, it is clear that additional model complexity exceeds the information that can be extracted from the primary calibration data. In this case increased model complexity does not provide further insights into dispersal. The Brownian motion of identical individuals described above serves as a simplified version better suited to existing data availability. This model will not be evaluated further; however it may provide a better starting point for future research.

4. Discussion

4.1. Proposed dispersal mechanisms

Dispersal behaviors of insects are determined through natural selection. Traits that result in maximization of successful reproduction are

Table 2
Calibrated model parameters for Brownian motion.

Location	Cohort	n/riffle	δ	G	p value
1	1	1960	3.5	38.7	0.00 ^a
1	2	1730	2.8	0.34	0.84
2	1	970	6.0	0.09	0.96
2	2	1740	2.5	0.30	0.86

^a Result not significant; calibrated model a poor predictor of trap counts.

Table 3
Lévy flight final calibration parameters.

Location	Cohort	n/riffle	α	G	p value
1	1	2500	0.35	1.168	0.56
1	2	5700	0.27	0.749	0.69
2	1	2090	0.35	0.004	0.99
2	2	6900	0.283	0.072	0.96

maintained. An insect population that disperses over large distances has an evolutionary advantage by reducing interbreeding, exploiting new habitats, or moving away from unfavorable conditions. The costs of dispersal however include increased risk of not finding a suitable habitat, encountering predators and a reduced possibility of finding a mate (Bilton et al., 2001).

Dispersal capabilities are an accumulation of traits developed over generations, such as wing length in Plecoptera and Ephemeroptera. Observed variation in wing length within these two orders suggests that dispersal has had varied importance in survival among different species. Some species have relied less on dispersal for survival, and therefore naturally possess weaker dispersal capabilities (Malmqvist, 2000). Brownian motion and Lévy flight each suggests different flight behaviors and consequently different tactics for surviving environmental disturbance. A Brownian motion based random walk results in limited lateral dispersal, which suggests a species adapted to endure adverse environmental conditions. A Lévy flight demonstrates more lateral dispersal, suggesting a species that survives by avoiding disturbance through exploitation of spatially separated habitats (Fig. 4).

Calibration results of both the Brownian motion and Levy flight model are presented above. Results of the calibration suggest that the Lévy flight and Brownian motion may both provide a sufficient explanation for stonefly behavior, however the Lévy flight model as the dispersal mechanism was a stronger predictor of field observations (Tables 2 and 3). As noted in Section 3.2, a model employing Brownian motion incorporating variations among individuals was capable of producing statistically significant calibration results when compared to field observations; however the presence of multiple parameter value optima suggests model complexity exceeded the information that could be extracted from the trap counts.

Through a mark and recapture study Macneale et al. (2005) found that adult females of *L. ferruginea* had dispersed up to 560 m laterally within one generation. The model was run with best fit parameter values to estimate the probability of long distance lateral dispersal (Fig. 4). The probability of an individual stonefly dispersing laterally 560 m or more through the calibrated Brownian motion model is

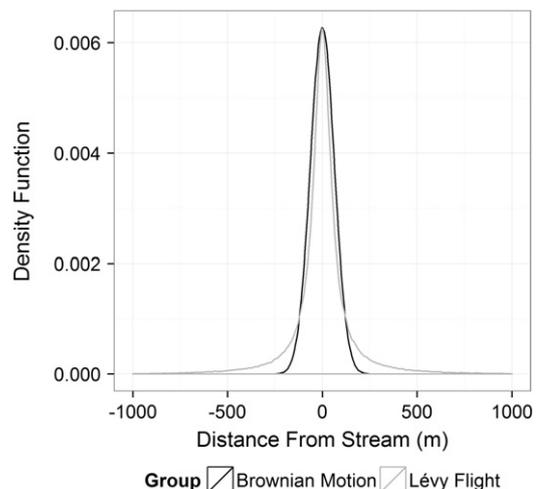


Fig. 4. Estimated density function for lateral dispersal distance of an individual under Lévy Flight ($\alpha = 0.313$) and Brownian motion ($\delta = 3.7$); result of 300,000 model iterations.

estimated as $9e - 13$. Through the calibrated Lévy flight model the probability of an individual dispersing at least 560 m or more laterally is estimated as 0.06 (Fig. 4).

Based on calibration results of field observations presented in this study as well as field observations by Macneale et al. (2005), the Lévy flight model provides the more probable approximation of female *L. ferruginea* dispersal behavior than Brownian motion.

Observations on the life cycle of *L. ferruginea* further support the selection of the Lévy flight model which demonstrates stronger dispersal behavior. A low pollution tolerance index (PADEP, 2012) and findings by Grubbs et al. (2006) that *L. ferruginea* eggs lack a diapause suggest that the species is not adapted to endure adverse or changing environmental conditions. Aquatic insect species lacking specialized traits to survive periodic disturbance are more likely to survive through a stronger ability to disperse and colonize new habitats (Bilton et al., 2001). These findings are suggestive of a taxon that has maximized survival efficiency through inter basin dispersal as a method of avoiding disturbance regimes, and one that would likely demonstrate more active dispersal.

4.2. Potential error sources

All models are inherently wrong, however, they can be useful in providing insights into natural phenomena that cannot be observed through practical means. As in all modeling work, error is introduced through a variety of sources: primary data used in model development, uncertainty in model parameter estimation and simplification of a natural process (Grant and Swannack, 2007). This section aims to describe, and if possible, quantify all potential sources of error.

Trap counts from 6 sticky traps along 2 transects represent the primary data set for model calibration in this study. It is noted that some specimens degraded significantly on the traps such that they could not be identified beyond the genus level. An inability to identify all *Leuctra* to species level compromised the validation dataset. Of all 859 EPT trapped, genus could be determined for 813 (94.6%) specimens. The error introduced through specimen degradation results in an error in the direction of under predicting total stonefly density and thus, leans in the conservative direction for estimating recolonization probabilities. The error in total trap count of *L. ferruginea* females at each location is underestimated by no more than 6% of the true trap count.

Given that the path of an insect incorporates some amount of randomness (Freeman, 1977; Petrovskii et al., 2011a,b) it is valid to assume that trap counts to be observed in a future field study are random variables with some unknown variance. The result of this modeling study suggests that the variances of the trap counts under this experiment design are non-negligible. A single year of field observations on stonefly dispersal may not provide a sufficient data set to quantify the variance inherent to trap counts resulting from the highly stochastic process of adult stonefly dispersal. Some error in model parameter estimation is assumed to exist due to this data limitation.

Maximum dispersal distance is a function not only of flight mechanisms for dispersal, but also time allowed for dispersal. As discussed above, the lifespan of adult *Leuctra* spp. is best described as a continuous probability distribution (Petersen, 2002). The simplifying assumption that lifespan of each individual is some constant average value would tend to under predict long distance dispersal events. Sensitivity analysis suggests that the probability of long distance dispersal events is sensitive to lifespan or simulation length. Dispersal within the vicinity of the trap locations used in this study, however, is not sensitive to life span. Model parameter estimation is not assumed to be compromised by this data limitation, however maximum dispersal distance may be underestimated by an unknown quantity.

Stonefly flight paths are continuous in nature, which can only be approximated through a random walk simulation. Random walks only estimate position at discrete moments in time. Kawaii and Petrovskii (2012) note that time step selection for a random walk model is critical

to obtaining meaningful results. Selection of an improper time step can lead to misinterpretations of the random walk. For example, at larger time steps non-correlated random walks, correlated random walks and Lévy flights all tend to produce similar results. Decreasing the time step may improve resolution of the flight path; however reaching the solution becomes more computationally intensive. Time step selection was guided in part by a desire to reduce the computational demand of the models. While a time step was chosen to minimize error through simplification of the random walk path, it is acknowledged that some amount of error was introduced none the less. Based on a sensitivity analysis of model time step this error is assumed to be negligible.

The model was simplified by excluding all environmental variables. As stoneflies have physical barriers to motion, natural predators, feeding requirements, mating requirements, etc. they have real observable interactions with the physical world. Assuming that stonefly flight direction is in no way influenced by the environment introduces some degree of error that cannot be quantified at the present. Two studies of stonefly dispersal versus varying types of natural environment resulted in no significant correlation (Griffith et al., 1998; Petersen et al., 2004). The effects of the urban environment on adult aquatic macroinvertebrate behavior remain largely unstudied. As artificial lighting and reflective surfaces have been shown to attract aquatic insects it is critical to understanding the probability of successful inter-basin transfer of ova (Horvath et al., 2009; Kriska et al., 2009; Malik et al., 2008; White and Shardlow, 2011).

4.3. Adult stonefly flight direction preference

As stoneflies require flowing water for successful reproduction (Hitchcock, 1973), it would be logical to assume that adult stoneflies exhibit some preference for maintaining a close proximity to flowing water throughout the entire adult lifespan. Several studies have proposed that stonefly flight is primarily along the riparian corridor, with limited lateral dispersal (Griffith et al., 1998; Macneale et al., 2005; Petersen et al., 1999, 2004). While it has been well established that upstream movement of adults occurs, these studies do not necessarily suggest a behavior with respect to lateral distance from the stream. Within this modeling exercise, simulated *L. ferruginea* females confined to a transect with no preference for flight direction accurately reproduced field observations. This suggests that *L. ferruginea* females may not need to exhibit a preference for flowing water during the adult life stage.

As *L. ferruginea* emerge from a stream, it is likely that many adult females will reencounter that stream purely through random movements. As all *L. ferruginea* emerge along a given stream it is probable that the highest density of *L. ferruginea* would remain centered along the stream corridor (Fig. 4) as a consequence only of their emergence location, relatively short lifespan and poor flight capabilities; not necessarily through a flight direction preference demonstrated during the adult life stage.

In an experiment of adult EPT, Macneale et al. (2005) noted that adult female *L. ferruginea* were captured with extruded egg masses attached to their abdomens at traps extending laterally from the stream. This suggests that the female stoneflies were within minutes of oviposition and not within the stream corridor. At the population level, research by Bunn and Hughes (1997) further supports this concept. Genetic analysis of stoneflies suggests that the entire larval population of a stream reach can be accounted for by oviposition of only a few females. They conclude that the stochastic effects of recruitment are a key factor that defines the aquatic community structure.

Within the calibrated Lévy flight model an estimated 50% of all adult female *L. ferruginea* will remain within 60 m of the stream of emergence. The simulated results of adult *L. ferruginea* females suggest that for a large population, purely random flight direction provides a sufficient rate of reencounter with the stream of emergence. Though females must find flowing water for oviposition, it may be necessary for some

aquatic insects to actively disperse away from water (Bilton et al., 2001). As *L. ferruginea* has a poor tolerance for changes in environmental conditions (Grubbs et al., 2006; PADEP, 2012) having no preference for flight direction may be a critical trait for survival.

4.4. Maximum probable dispersal distance

Estimating rates of recolonization of *L. ferruginea* within Philadelphia, PA are critical to designing post stream restoration monitoring programs. Post restoration recolonization will likely occur through gradual progression as restored streams adjacent to existing *L. ferruginea* populations are recolonized. Recolonized streams would then serve as population sources allowing subsequent generations to disperse further.

The Schuylkill Center for Environmental Education is conservatively assumed to be the only existing source of *L. ferruginea* in the Philadelphia area. Rapid bioassessments of many smaller streams sampled relatively few EPT specimens with *Leuctra* spp. specimens collected only within French Creek approximately 40 km Northwest of Philadelphia (PWD, 2004).

The Lévy flight random walk model calibration yielded shape parameters in the range of 0.27 to 0.35 (Table 3). Based on population density estimates and an average Cauchy shape parameter value (.313) (Section 3.3), the estimated maximum probable distance for successful dispersal by *L. ferruginea* within 1 generation is 2100 m. This result suggests that streams further than 2100 m from a known source may require additional considerations for successful reintroduction of *L. ferruginea*.

5. Conclusions

- 1) Through a one year field study of adult EPT insects 15 taxa were trapped, all demonstrating some degree of lateral dispersal. *L. ferruginea* was selected for further study as the taxon was most numerically abundant on the traps and exemplified more active dispersal relative to other EPT taxa.
- 2) The methods presented demonstrate a simulation based approach to estimating stonefly dispersal behavior. Simulations of dispersal provide an improvement over more commonly employed statistical models. Examination of a group of previously employed models of insect dispersal suggests that individual based random walk models with modifications presented in this paper are most applicable to modeling adult stonefly dispersal.
- 3) Each of the proposed mechanisms for stonefly flight, Brownian motion and Lévy flight, was capable of reproducing observed trap counts. The Lévy flight model proved to be a better fit when compared with mark and recapture observations (Macneale et al., 2005) as well as conceptual observations made on stonefly life cycles and behavior (Bunn and Hughes, 1997; Grubbs et al., 2006; Hitchcock, 1973). The Lévy flight suggests that stoneflies may exhibit specialized searching techniques as opposed to non-specialized Brownian movement.
- 4) Estimates within this paper suggest that overland dispersal may be a viable pathway for successful dispersal to adjacent streams by *L. ferruginea* if the restored stream is within 2100 m of a known source. In order to predict the rate of dispersal to a specific stream reach, however, local conditions such as required dispersal distances, the sequence of stream restoration and resulting habitat segmentation must be taken into consideration.

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