



VCU

Virginia Commonwealth University
VCU Scholars Compass

Theses and Dissertations

Graduate School

2014

Forest edges enhance mate-finding in the European gypsy moth, *Lymantria dispar*

Lily Thompson
Virginia Commonwealth University

Follow this and additional works at: <https://scholarscompass.vcu.edu/etd>



Part of the [Biology Commons](#)

© The Author

Downloaded from

<https://scholarscompass.vcu.edu/etd/606>

This Thesis is brought to you for free and open access by the Graduate School at VCU Scholars Compass. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of VCU Scholars Compass. For more information, please contact libcompass@vcu.edu.

© Lily M. Thompson, May 2014

All Rights Reserved

Forest edges enhance mate-finding in the European gypsy moth, *Lymantria dispar*

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
in Biology at Virginia Commonwealth University.

By

Lily M. Thompson
Bachelor of Science, Centre College, 2010

Thesis Advisor: Derek M. Johnson, PhD,
Assistant Professor, Department of Biology

Virginia Commonwealth University
Richmond, Virginia
May 2014

ACKNOWLEDGEMENT

Success is very rarely achieved in isolation and the success I have achieved in my Master's degree program is no exception. I would like to thank my advisor, Dr. Derek Johnson, who has been an invaluable teacher, coach, mentor, and supporter throughout the process. Thanks also to Dr. Kristine Grayson whose knowledge and experience have enhanced many brainstorming sessions. Many thanks to everyone at Blandy Experimental Farm (University of Virginia; NSF FSML Grant (DBI 1034846)) who helped make my field work a success. Thanks to the Center for Plant Health Science and Technology, Otis Lab (USDA, APHIS, Otis ANGB, Buzzards Bay, MA) who graciously provided the gypsy moth subjects for my study. To my committee members, Dr. Lesley Bulluck, Dr. Daniel McGarvey, and Dr. James Vonesh: I could not have asked for more knowledgeable and well-rounded scientists to be on my team. Thanks also to the Virginia Commonwealth University Biology Department for the opportunity to deepen my understanding of science through their Master's program. I am ever grateful for the members of the population & community ecology lab group for their unwavering support, friendship, and knowledge sharing. Finally, I would like to thank my family and friends who have always believed in me and encouraged me to pursue my dreams. This would not have been possible without all of you.

TABLE OF CONTENTS

List of Tables	v
List of Figures	vi
Abstract	vii
Introduction	1
Methods	3
Study system	3
Release-recapture design	5
Experimental design	6
Study area	7
Weather data collection and analysis	8
Vegetation data collection and analysis	8
Among array data analysis	8
Within array data analysis	9
Results	9
Weather	9
Vegetation	10
Among array comparisons	10
Within array comparisons	10
Discussion	12

Tables	16
Figures.....	18
Literature Cited	28
Appendix.....	32
Vita.....	33

LIST OF TABLES

Table 1. Weather data collected over the duration of the experiment	16
Table 2. Vegetation data summarized by site for each array type	17

LIST OF FIGURES

Figure 1. Female-baited delta trap configuration.....	18
Figure 2. Experimental design	19
Figure 3. Map of general locations of trap arrays at Blandy Experimental Farm	20
Figure 4. Effects of weather variables on proportion of male recaptured	21
Figure 5. Effects of proportion canopy cover on proportion of male recaptured	22
Figure 6. Line graph of among array comparisons using predicted values	23
Figure 7. Line graph of within forest array comparisons using predicted values.....	24
Figure 8. Line graph of within field edge array comparisons using predicted values	25
Figure 9. Line graph of within forest edge array comparisons using predicted values	26
Figure 10. Line graph of within field array comparisons using predicted values.....	27

ABSTRACT

FOREST EDGES ENHANCE MATE-FINDING IN THE EUROPEAN GYPSY MOTH, *LYMANTRIA DISPAR*

By Lily M. Thompson, BS

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Virginia Commonwealth University, 2014.

Thesis Advisor: Derek M. Johnson, PhD, Assistant Professor, Department of Biology

Understanding movement capabilities of individuals within a landscape is essential to identifying the effects of habitat boundaries on species abundances, ranges, and spread rates. Movement barriers due to habitat fragmentation may reduce mate-finding ability in some species, particularly in heterogeneous landscapes containing low-density populations. This study focuses on the effects of habitat type and edge on mate-finding in an invasive defoliator, the European gypsy moth. Adult European gypsy moth males locate mates by following pheromones released by flightless females. Reduced mate-finding was expected in fields and near forest edges based on geographic variation in invasion rates and pheromone plume dynamics. A male release-recapture experiment using female-baited traps in fields, at forest edges, and in the forest interior showed that mate-finding was highest at forest edges, reduced in fields, and lowest within the forest interior. This suggests that forest edges and moderate habitat fragmentation enhance mate-finding in the gypsy moth.

INTRODUCTION

Understanding the movement of individuals within a landscape is essential to identifying how habitat boundaries may influence species ranges (Bascompte et al. 1996). Most landscapes are heterogeneous mosaics of habitat types or successional stages with varying levels of discontinuity, and the permeability of boundaries between these landscape elements is species-specific (Wiens et al. 1985). In areas of low permeability, a species may be effectively trapped within isolated populations. Alternatively, in areas of high permeability, movement of individuals within the landscape is determined by biological characteristics, such as mating behavior, foraging behavior, and sociality, instead of physical barriers (Dover & Settele 2009).

Habitat fragmentation decreases the size of habitat patches and, in some cases, can increase the distance between habitat patches (Fahrig 2003). Small fragments have a high perimeter to area ratio, and may effectively function as entirely habitat edge or merge with the surrounding non-habitat area (Ries & Sisk 2004). Heterogeneities in landscape structure can have multiple effects that act across spatial scales (Stephens et al. 2003). For instance, population density in a habitat fragment is mediated by potentially conflicting cross-scale effects, such as variation in resource quality, natural enemies, and net emigration (Thomas et al. 2001; Menéndez et al. 2002; Stephens et al. 2003).

The role of habitat edges in shaping species abundances and movement patterns is well documented (e.g., MacArthur & Wilson 1967; Wiens et al. 1993; Fahrig 2003). The effect of

habitat edges is species-specific and can be context-dependent (Unfried et al. 2013). Some species, like woody tropical vines (lianas), prefer or require habitat edges and fragmentation may be beneficial for those species (Laurance et al. 2001; Fahrig 2003). Other species may be negatively affected by habitat edges or not affected at all (Ries & Sisk 2004; Fahrig 2003). Edges may exhibit characteristics of one of the adjoining habitat types or a combination of them (Ries & Sisk 2004).

The degree to which fragmentation is detrimental depends on whether unsuitable habitat poses a barrier to the movement, survival, or reproduction of individuals. The term “matrix” is often used to describe unsuitable or non-focal habitat and this area is generally considered barren; however, for some species the matrix may contain resources, but in lower quantity or quality (Bender & Fahrig 2005). If crossing the matrix is disadvantageous due to physical or physiological constraints, resource limitation, or increased predation risk, a population may become isolated (Wiens et al. 1993). Habitat corridors can help prevent isolation in some species, but the risk of isolation is amplified in species that innately have limited mobility (Haddad & Tewksbury 2005; Öckinger & Smith 2007). Isolation can result in decreased fitness caused by decreased resource availability, inbreeding, and reduced mate-finding (Aars & Ims 2000).

Mate-finding is essential for the persistence and spread of a population and may be highly impacted by habitat fragmentation (Contarini et al. 2009). Specifically, mate finding can be reduced when structural changes caused by habitat fragmentation result in low-density populations (Gascoigne et al. 2009) or when the structural changes themselves disrupt normal aggregation of individuals, movement capability, or mating cues, such as pheromone signals or mating displays (Harrisson et al. 2013). When habitat fragments are small and the matrix is

permeable, emigration may decrease the size of a population in a given patch (Menéndez et al. 2002). Without balanced immigration, dispersal from small habitat fragments may magnify rates of mate-finding failure (Contarini et al. 2009). Mate-finding failure can be a component Allee effect, where a positive relationship occurs between population size and fitness, which can ultimately result in population decline or extinction at low population densities (Menéndez et al. 2002).

How habitat edges affect mate-finding in low-density populations is of particular interest for understanding the population dynamics of rare species, range edges, and invasion fronts, all of which are inherently operating at low-densities. However, low-density populations are difficult to study because individuals are difficult to detect. Reliable techniques using pheromone-baited traps have been developed to detect an important invasive defoliator, the European gypsy moth (*Lymantria dispar*), at very low-densities making it an ideal system to study low-density population dynamics (Sharov & Liebhold 1998). In this study, I compare mate-finding success of adult male gypsy moths at locations within a forest fragment, near the forest edge, and outside a forest fragment in order to assess the effect of habitat edges on gypsy moth mate-finding capabilities.

METHODS

Study system: The European gypsy moth (hereafter, “gypsy moth”) was introduced near Boston, Massachusetts, USA in 1869 and has since become a high-impact, invasive species across the Eastern United States and Canada (Elkinton & Liebhold 1998). Outbreaks of the gypsy moth in established regions cause recurrent forest defoliation resulting in ecological,

economic, and aesthetic damage (Elkinton & Liebhold 1990; Sharov & Liebhold 1998). Gypsy moth densities typically exhibit cyclical population dynamics both along the invasion front and in established areas, and are very low in most years (Haynes et al. 2009). The United States Forest Service keeps detailed records of past and current defoliation events while annually maintaining a trapping scheme at the invasion front to assess population spread using pheromone-baited traps able to detect gypsy moths at very low densities, (Sharov & Liebhold 1998). The main dispersal mechanisms for gypsy moths are anthropogenic movement of juvenile life stages and larval ballooning, while adult male flight can lead to dispersal of genetic material, but not population establishment (Elkinton & Liebhold 1990).

Gypsy moths express a sex-specific dispersal polymorphism in which flightless females attract flying males through pheromone release (Elkinton & Liebhold 1990; Murlis et al. 2000). Gypsy moth adults live approximately one week and do not feed. Adult females attract males by releasing pheromones in pulses from a small gland near the tip of the abdomen shortly after emergence. The quality of the pheromone signal decreases after three days and females stop producing pheromone after mating (Leonard 1981). After mating, females find a suitable oviposition site and lay a single egg mass (Doane 1968).

In order to find females, male gypsy moths follow pheromone signals using visually assessed movement and correcting for drift away from the pheromone source, known as optomotor anemotaxis (Murlis et al. 2000; David et al. 1983). Pheromone detection is the principal mode of mate location, but this is supplemented by visual cues allowing for parallel movement with the ground and for detecting vertical objects on which females might be perched (Willis et al. 2004; Murlis et al. 2000; Charlton & Cardé 1990). Male gypsy moth movement is greatest during daylight hours (Murlis et al. 2000; Leonard 1981). Adult male gypsy moths have

reduced effectiveness at locating the source of pheromones when plumes are homogeneous (Murlis et al. 2000). Females produce pheromones in pulses and the maintenance of this heterogeneity in the signal allows males to more accurately assess the direction of the females (Murlis et al. 2000). Plumes tend to be more homogeneous in fields than in forests, particularly as the distance from the pheromone source increases (Murlis et al. 2000).

Due to the difficulty of rearing females and the ease of using synthetic pheromone, most current studies on male dispersal and mate-finding use synthetic pheromone baited traps. Synthetic pheromones are up to 1,000 times stronger than natural pheromones, and released steadily, thus, many trapping experiments using synthetic pheromones may not represent mate-finding in natural populations. Males can disperse up to 800m, but male recapture rate is very low at this distance (0.1-0.2%; Mastro 1981). A study using traps baited with 50 females each showed 1.5% recapture rate at 50m from release (Mastro 1981).

Release-recapture design: Lab-reared, virgin female adult gypsy moths were used to bait delta traps in a mosaic of fragmented forest habitat where lab-reared male adult gypsy moths were released. In this experiment, the focal habitat is the forest and the matrix is an adjacent field. Female-baited delta traps were used instead of synthetic pheromone-baited carton traps in order to more accurately imitate natural field conditions. Gypsy moth pupae were obtained from the Center for Plant Health Science and Technology, Otis Lab (USDA, APHIS, Otis ANGB, Buzzards Bay, MA) and were allowed to develop and emerge in the lab with males and females isolated from each other. All adults used in experiments had emerged within approximately 24 hours. Two females were placed in each trap inside a hardware cloth cage to ensure they did not escape or mate, thus ceasing pheromone production, during the study (Figure 1a). On five occasions, only one female per trap was used due to limited emergence. The number of females

per trap in any given release was consistent. Each female was used in only one release and no females suspected of being mated were used in the field. The interior of all delta traps was coated in Tanglefoot®, a sticky adhesive, which is designed to catch males entering the trap (Figure 1a).

Based on availability from emergence, between 62 and 477 male gypsy moths (mean = 219) were released at a release point and collected in traps for a 24-hour time period. Males that did not leave a release point within 24 hours were collected and subtracted from the number of males originally released and this difference was recorded as the number of flight males. Mate-finding success was determined by the number of male moths recaptured in the female-baited delta traps (Appendix: Table 1).

Experimental design: Four array types were used for this experiment (Figure 2). Each array was semicircular and consisted of a release point and 10 traps. Delta traps were equally spaced in a 180° semicircle array with a 25m radius from the release point (traps approximately 8.7m apart). This distance was used to maximize recapture rates and capture small scale mate-finding behavior (Maestro 1981). Each trap was placed approximately 1.25m from the ground and attached to a ¾ inch PVC pipe (Figure 1b). Three array types were near the forest edge, delineated by a tree line. In these arrays, release points were located either 15m inside a forest fragment or 15m outside a forest fragment, in an adjacent field (Figure 2). Two of those trap arrays spanned the tree line: field edge array (field release, edge facing traps) and forest edge array (forest release, edge facing traps). The third was a field array (field release, field facing traps), which used the release point 15m outside of the forest (in the field) with of traps farther into the field (Figure 2). Each array type near the forest edge was repeated three times at each of three sites in the study area (Figure 3). The fourth array type consisted of releases in the interior

of a forest fragment with a semicircle array of traps facing east and another facing west (forest interior array). There were two releases in each forest interior array direction.

Each array type was further divided into five trap types based on relative position within the array with two traps of each type (Figure 2). For the forest edge and field edge arrays these trap types were field, field/edge, edge, forest/edge, and forest. In the field array, trap types were numbered 1 through 5 with higher numbers referencing a farther distance from the tree line (Figure 2). Forest interior array trap types were also numbered 1 through 5, where 1 represents the ends of the semicircular array and 5 represents the center of the semicircular array (Figure 2).

Study area: The study took place at the University of Virginia's Blandy Experimental Farm in Boyce, VA. Located in the Shenandoah Valley, Blandy is within the current gypsy moth range and inside the gypsy moth quarantine zone. Releases took place from June 18, 2013 through August 7, 2013, with no releases from June 22, 2013- July 19, 2013 to avoid the natural flight period of gypsy moths in the area. This allows for confidence that all the males caught were released as part of the study and the experimentally released males did not mate with females in the natural population.

The area is a mosaic of agricultural land and mixed hardwood forest stands. Three sites (horse trail, soybean field, and cow pasture) were selected for arrays near the forest edge based on distinctness of tree line and directional orientation: one borders forest to the west, one to the east, and one to the south (Figure 3). Due to time constraints, there was only one release at the cow pasture site (forest to the south). The forest interior array site was selected because it was the most interior forest location in the study area with the most visually dense canopy cover that would not interfere with releases at experimental sites. All proper permits to transport and release gypsy moths were obtained from the USDA.

Weather data collection and analysis: Microclimate variables, including daily wind direction, wind speed, rainfall, and temperature (high, low, average) were measured at each release point using a Davis Instruments Vantage Pro 2 Precision Weather Station. Blandy Experimental Farm also collects daily weather data on temperature (high, low, average) and rainfall, but not wind. Weather data from the release points were compared to weather data recorded by Blandy Experimental Farm using Welch's two sampled t-tests to determine if there were significant differences between weather at the study sites and the weather in the general area. Linear regression models were used to analyze the relationship between the proportion of males recaptured on a given day and the weather (high, low, and mean temperature and total rainfall).

Vegetation data collection and analysis: Vegetation at each trap and release point was characterized by 7 vegetation parameters: groundcover (grasses and forbs), small shrub (<1m), large shrub (>1m), small sapling (<1m), large sapling (>1m), tree (>10cm DBH) and canopy cover. Presence/absence of these vegetation parameters was recorded at each of four points 1m from a trap/release point in the cardinal directions. Data from these points were then combined to give a proportion cover estimate of each parameter for a given location. The relationship between proportion canopy cover and male recapture was analyzed using linear regression.

Among array data analysis: Total male gypsy moths recaptured among array types was assessed using a generalized linear mixed model with fixed effects of array type, number of flight males and number of females per trap, with site and release day as random effects. The random effect of site accounts for inherent differences between the sites including vegetation and compass orientation. The random effect of day accounts for temporal variation in weather and

other environmental conditions during the study. Significant differences ($p < 0.05$) in male recapture among array types were determined.

Within array data analysis: The effect of trap type within an array was assessed using a generalized linear mixed model. Trap type, number of flight males, and number of females per trap were fixed effects and site and release day were random effects. Site accounts for inherent differences (vegetation and orientation) among the sites. Release day again accounts for temporal variation in the environment (e.g., weather). All statistical analyses were conducted in R version 2.15.1 at a significance level of $p < 0.05$.

RESULTS

There were between 61 and 384 flight males for each release across the study (mean = 207.12; Appendix: Table 1). Between 1 and 127 males were recaptured during each release (mean = 29.92; Appendix: Table 1). Recapture rates per release during the experiment ranged from 1.64% to 33.07% with a mean of 13.02%. This was at or above the expected recapture for the experiment.

Weather: Mean daily temperatures for the duration of the experiment ranged from 18.27°C to 26.87°C with an average mean daily temperature of 22.58°C (Table 1). Daily rainfall totals ranged from 0-1.06 inches over the summer with an average daily rainfall of 0.12 inches (Table 1). Due to equipment malfunction, weather variables from the release point were unavailable for 7 releases. Weather data collected by Blandy Experimental Farm included maximum temperature, minimum temperature, mean daily temperature, and daily rainfall. A Welch's Two Sample t-test showed that of the 4 variables collected at the release points and by

Blandy (high, low, and mean temperature, and daily rainfall), only maximum daily temperature was significantly different between the weather sources ($t = -1.9844$, $df = 41.79$, $p = 0.054$). The difference in means of the maximum daily temperature was only 2°C ; this was considered a small enough difference to supplement the missing data from the release points with the Blandy weather data (Table 1). Blandy weather data were also used for the daily rainfall totals.

The proportion of males recaptured on a given day was plotted against daily temperature and rainfall data (Figure 4). There was not a significant effect of any of these variables on the proportion of males caught (all p 's > 0.05 ; Figure 4). Therefore, weather variables were not included as random effects in the recapture models. Wind variables were not analyzed directly because the mirrored nature of the experimental design accounted for variation in wind direction during the study (Figure 2).

Vegetation: Grass and forb vegetation as a combined groundcover measure comprised the majority of vegetation at all sites (Table 2). The relationship between proportion canopy cover and the proportion of males recaptured at a given site was analyzed because of the close association between gypsy moths and trees, particularly in immature life stages. The relationship was approaching significance ($R^2_{\text{adj}} = 0.027$, $F_{1, 82} = 3.269$, $p = 0.074$), suggesting that traps with more canopy cover caught more males over the course of the experiment (Figure 5).

Among array comparisons: Significantly more males were recaptured in the field ($p = 0.002$), field edge ($p < 0.001$), and forest edge ($p < 0.001$) array types than in the forest interior array type (Figure 6). The field, field edge and forest edge array types were not significantly different from each other (all p 's > 0.4198).

Within array comparisons: Trap types based on trap density in the forest interior array were analyzed to determine if the experimental design biased the results, i.e., do traps at the end

of the semicircular array catch more or fewer moths than interior traps. There was not a significant difference in number of males caught among any of the trap types in the forest interior array (all p 's > 0.18 ; Figure 7). Therefore, these data show that position of a trap within the array did not affect recapture rate independent of trap type effects.

In the field edge array, the number of recaptured males per trap type increased monotonically from the field to the forest (Figure 8). Forest traps in the field edge array had significantly higher male recapture than any of the other trap types (all p 's < 0.03). Forest/edge and edge trap recaptures were not significantly different and there were significantly more males recaptured in these trap types than in either the field/edge ($p < 0.001$) or the field traps ($p < 0.001$). Significantly more males were recaptured in the field/edge traps than in the field traps in the field edge array ($p < 0.001$). All releases of this array type used 2 females per trap, so this parameter was excluded from the model. The number of flight males in the field edge array releases was significant ($p < 0.001$).

In the forest edge array, there were significantly more males caught in the forest than in any other trap type (p 's ≤ 0.01 ; Figure 9). There were no significant differences among field, field/edge, or edge trap recaptures (all p 's ≥ 0.71). There were significantly more males recaptured in the forest/edge traps than in the edge ($p = 0.0023$), field/edge ($p < 0.001$), or field (< 0.001) trap type. The number of flight males in releases in the forest edge array was significant ($p < 0.001$). All releases in this array type included 2 females per trap, so that parameter was excluded from the model.

In the field array, there were significantly more males recaptured in the trap type closest to the forest (trap 1) than in the two trap types farthest from the forest (trap 4 ($p = 0.005$) and trap 5 ($p = 0.041$); Figure 10). The number of males recaptured in trap 1, trap 2, and trap 3 (the three

closest to the forest) was not significantly different (all p 's ≥ 0.11). Trap 2 (second closest to forest) had significantly fewer males recaptured than trap 3 (middle distance to forest, $p = 0.0058$) and significantly more than trap 4 ($p = 0.016$), but was not different than trap 5 (farthest from forest, $p = 0.386$).

DISCUSSION

Understanding how habitat fragmentation impacts the movement of individuals within a landscape is important to understanding the progression of species' ranges. Movement capability and how it affects mate-finding is of particular interest for understanding how invasive species, such as the gypsy moth, establish and increase their range. This study suggests that mate-finding success in the gypsy moth is higher near forest edges than in the forest interior (Figure 6). This enhanced mate-finding was particularly pronounced 15m inside of the tree line, as seen by the high recapture of males in the forest trap types of the forest edge array (Figure 9). While males may be better at finding females as the proportion of canopy cover increased (Figure 5), the field had higher mate-finding success than forest interior locations in our study (Figure 6).

Patterns of recapture in releases from the field (field array and field edge array) suggest that males may be cuing in to landscape characteristics in habitat edge environments in addition to pheromone plumes in order to maximize mate-finding. Males were recaptured more often in the traps closest to the forest when males were released from the field, even when no females were in the forest (Figure 10). Furthermore, trap array structure was not seen to impact the proportion of recaptured males per trap as measured in the forest interior array (Figure 7).

Together, this may suggest that males are using visual landscape characteristics as well as pheromone cues to direct their movement. However, the distinction between landscape characteristics and pheromone cues cannot be fully disentangled in this study due to the nature of female-baited trap recapture methods.

Results from this study suggest that males will traverse field habitat up to 25m in response to females, but are less successful at mate-finding in a field compared to forest edge habitat (Figures 6, 8, & 9). Additionally, males that were released in the field were able to find females farther into the field (Figure 10); however, the scale of this movement is very small compared to the flight capabilities of the gypsy moth. Additionally, this study used traps attached to PVC pipe in the field, creating artificial vertical structures. While some studies claim that males exhibit vertical tracking behavior near a pheromone source (David et al. 1983), others dispute this, suggesting that males cue in on vertical cylinders, but observed “tracking” behavior is an artifact of plume structure near tree trunks (Willis et al. 1994). Therefore, it is unclear if the results found here would be observed if there were no natural vertical structures (e.g., trees) in the field or whether egg masses laid in the field would produce successful offspring.

Previous research on gypsy moth pheromone plumes and pheromone reception suggests that mate-finding would be higher in the forest interior rather than the field habitat because of the homogenization of the pheromone signal in the field (Murlis et al. 2000). The results presented here do not support those findings; mate-finding success, measured by male recapture, was lower in the forest interior array than in any of the others. Localized forest structure could have an impact on the shape and dispersion of the pheromone plumes and, thus, the success of mate-finding. In this study, I measured only one forest interior plot and it had a considerable amount of understory vegetation in addition to having a high proportion of canopy cover. The effect of

forest structure on pheromone signaling is something that could not be tested here, but future work including more detailed vegetation sampling could help elucidate this phenomenon.

While an agricultural landscape with relatively well-defined tree lines was used in this study, the results illustrate the difficulty of differentiating between distinct physical landscape boundaries and functional edge habitat. The traps categorized as edge types from the forest edge and field edge array were located at the tree line; however, mate-finding success was lower in those traps than in the forest trap types of the same arrays. This suggests that the functional habitat edge for the gypsy moth is more broadly defined by edge effects rather than an abrupt physical landscape change. Therefore, all the trap types in the forest edge array and field edge array are likely functioning within a gradient of forest edge habitat rather than specifically forest interior or field habitat. Bellinger et al. (1989) and Campbell et al. (1976) found increased egg-mass presence near forest edges. The data presented here supports this data by providing evidence that the increased ability of male gypsy moths to find females near the forest edge could explain why more females, and thus egg masses, are found near forest edges.

The quality of the matrix surrounding a focal habitat is often a key factor in determining how permeable habitat edges are to movement of individuals and populations (Vandermeer et al. 2001; Haynes & Cronin 2006). For instance, the number of gypsy moth egg masses in a given area decreases as the quality of the matrix decreases (Vandermeer et al. 2001). This is particularly important to habitat connectivity and corridor usage for management purposes. Matrix quality does not necessarily need to be as good as focal habitat for species to be able to move between habitat patches (Haddad & Tewksbury 2005).

At the scale studied here, mate-finding in the gypsy moth is enhanced at forest edges and non-forested areas are semi-permeable to male moth movement. If this pattern is also observed at

a larger scale, it would suggest that habitat fragmentation may not be driving the observed geographical difference in range expansion of the gypsy moth at the invasion front, which is characterized by slower spread in the highly fragmented forests of Illinois, Indiana, and Ohio (Tobin et al. 2007). However, the scale studied here (25m) is very small compared to the dispersal capabilities of the moth, which can be up to approximately 800m (Mastro 1981). Therefore, these findings should be used to generate hypotheses, but not formulate conclusions about the effects of fragmentation at larger scales. For instance, this study may suggest that mate-finding success in the gypsy moth would be highest in forest fragments with a high perimeter to area ratio where more of the total area of the fragment was functioning as habitat edge. Consequently, gypsy moth invasion may follow forest edges in newly invaded areas.

Given the inherent difficulties of studying small, low-density populations, which are characteristic of an expanding range edge, gypsy moths offer a unique opportunity to investigate the mediation of mate-finding in small populations by landscape characteristics. While demographic Allee effects in the gypsy moth are strongest and invasion is the slowest in the regions with historically high fragmentation due to agriculture (Tobin et al. 2007), this study does not support the hypothesis that mate-finding failure is the underlying mechanism for the Allee effect. At the small scale of this study, habitat fragmentation may enhance mate-finding and increase invasion in gypsy moth populations.

TABLES

Table 1. Weather variables collected throughout the duration of the experiment (late June-early August) by day of the year. Unless otherwise noted, temperature data was collected within 3m of the release point of the array type tested on that day.

Day of Year	Maximum Temperature (°C)	Minimum Temperature (°C)	Mean Temperature (°C)	Total Rainfall (inches)**	Wind Speed (mph)	Wind Direction (degrees)
169	26.94	19.67	22.96	0.44	0.54	-71.22
170	30.28	19.56	22.39	0	0.35	248.01
171	26.11	16.67	19.67	0	0.10	-38.46
**175	33.00	19.00	26.00	0.01	+	+
**176	35.00	18.00	26.50	0	+	+
**177	33.00	18.00	25.50	0.05	+	+
**178	30.00	19.00	24.50	0.06	+	+
**179	33.00	17.00	25.00	1.06	+	+
200	34.28	22.72	26.87	0	1.47	186.73
201	33.22	21.44	26.73	0	2.92	207.58
202	23.39	20.44	21.73	0.11	0.56	199.67
**205	28.00	18.50	23.25	0	+	+
**206	25.00	15.00	20.00	0	+	+
207	27.72	12.83	20.11	0	0.72	222.33
208	26.22	16.44	21.86	0	0.40	191.35
209	28.78	19.00	22.95	0.26	0.50	-74.92
210	23.11	14.11	17.53	0	1.04	-46.10
212	23.56	19.56	20.99	0.4	0.04	217.14
*213	24.94	18.72	20.94	0.06	0.00	250.05
*214	29.11	17.17	21.46	0	0.27	239.96
215	20.94	16.67	18.97	0.2	0.00	230.99
216	25.33	15.89	20.05	0	1.65	28.83
217	23.83	12.50	18.27	0	0.25	268.88
218	22.94	17.28	19.84	0.07	0.00	-17.56
219	26.28	19.11	21.83	0.16	0.00	251.57
220	21.50	20.22	20.87	0.44	0.00	202.50

*Two releases on this day. Both releases were of the same array type in different locations

**All data from Blandy Experimental Farm, not from release point

+ Wind information unavailable

Table 2. Mean and standard deviation (in brackets) of vegetation parameters across all traps at each array type

Location	Groundcover	Small Shrub	Large Shrub	Small Sapling	Large Sapling	Tree (>10cm DBH)	Canopy Cover
Forest Interior	0.34 [0.28]	0.09 [0.15]	0.2 [0.31]	0.2 [0.28]	0.11 [0.17]	0.04 [0.09]	0.99 [0.3]
Horse Forest Edge	0.65 [0.34]	0.07 [0.12]	0.09[0.7]	0.09 [0.23]	0.07 [0.12]	0.05 [0.1]	0.77 [0.4]
Soybean Forest Edge	0.53 [0.34]	0.14 [0.21]	0.05 [0.1]	0.02 [0.08]	0.14 [0.3]	0.14 [0.3]	0.6 [0.49]
Horse Field Edge	0.7 [0.23]	0.05 [0.1]	0.09[0.23]	0 [0]	0.09 [0.17]	0.05 [0.1]	0.67 [0.38]
Soybean Field Edge	0.45 [0.42]	0.16 [0.28]	0.05[0.15]	0.05 [0.1]	0.07 [0.16]	0.07 [0.12]	0.5 [0.45]
Cow Field Edge	0.93 [0.12]	0 [0]	0 [0]	0 [0]	0 [0]	0.07 [0.12]	0.75 [0.35]
Horse Field	0.83 [0.17]	0 [0]	0 [0]	0 [0]	0.09 [0.13]	0.02 [0.08]	0.31 [0.40]
Soybean Field	1 [0]	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]

FIGURES

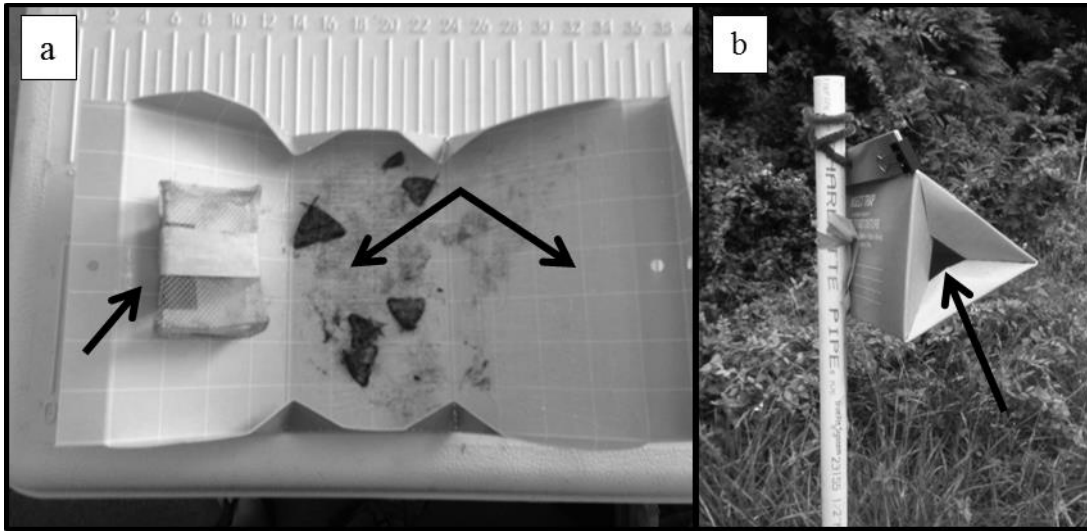


Figure 1. Female-baited delta trap experimental set-up. **a)** Inside of a trap. The arrow on the left points to the hardware cloth cage that holding females. The arrows on the right point to the sides of the trap coated with Tanglefoot®. **b)** Traps are secured to PVC pipe with pipe cleaners. The arrow points to the opening in one end of the trap. There is an identical opening on the other side.

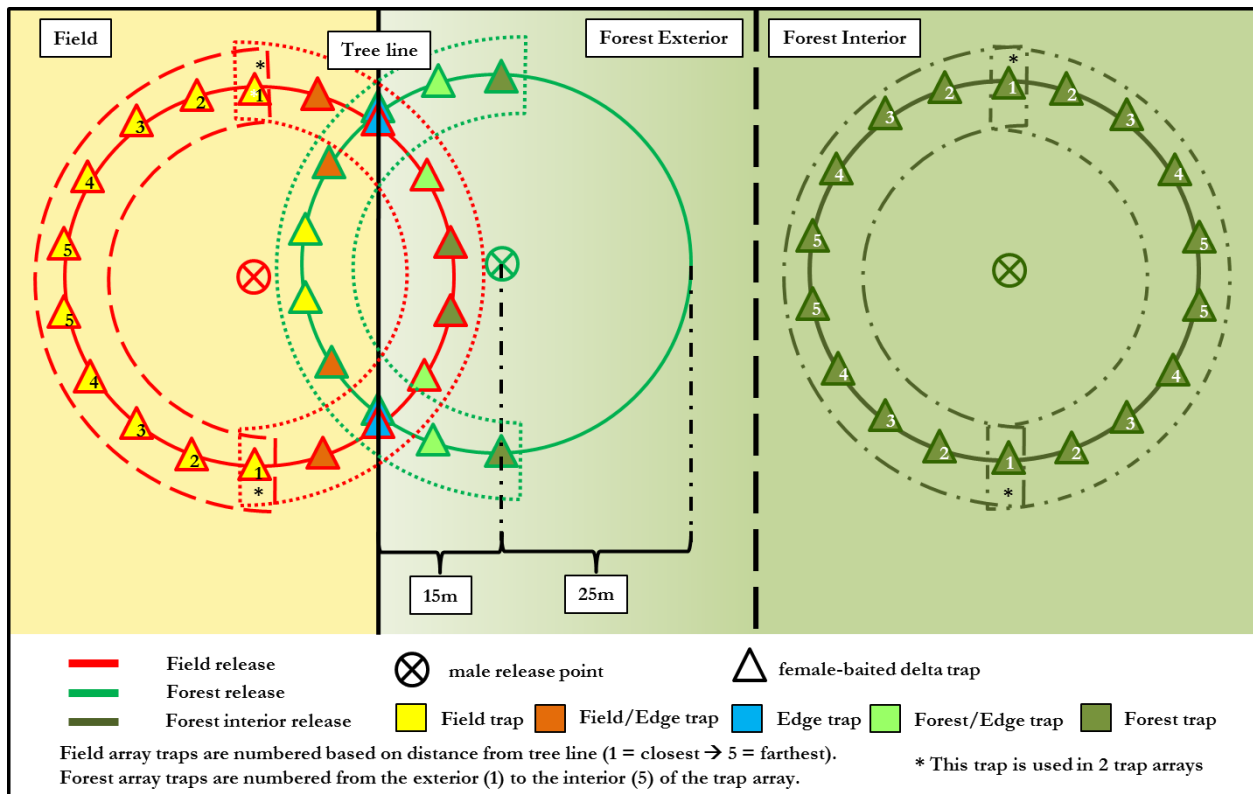


Figure 2. Graphical representation of the experimental design. Each trap array contained 10 female-baited traps, one male release point, and is notated in the figure by a semicircular outline. Male releases were replicated at each field and edge trap array at least three times per site. Male releases at the two forest interior arrays were replicated two and three times.

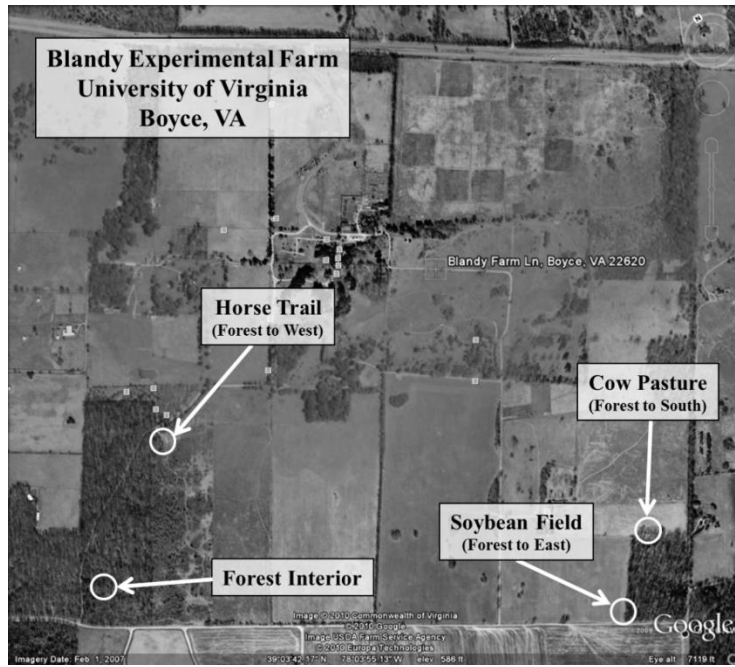


Figure 3. Map of general locations of array sites at Blandy Experimental Farm (University of Virginia) in Boyce, VA.

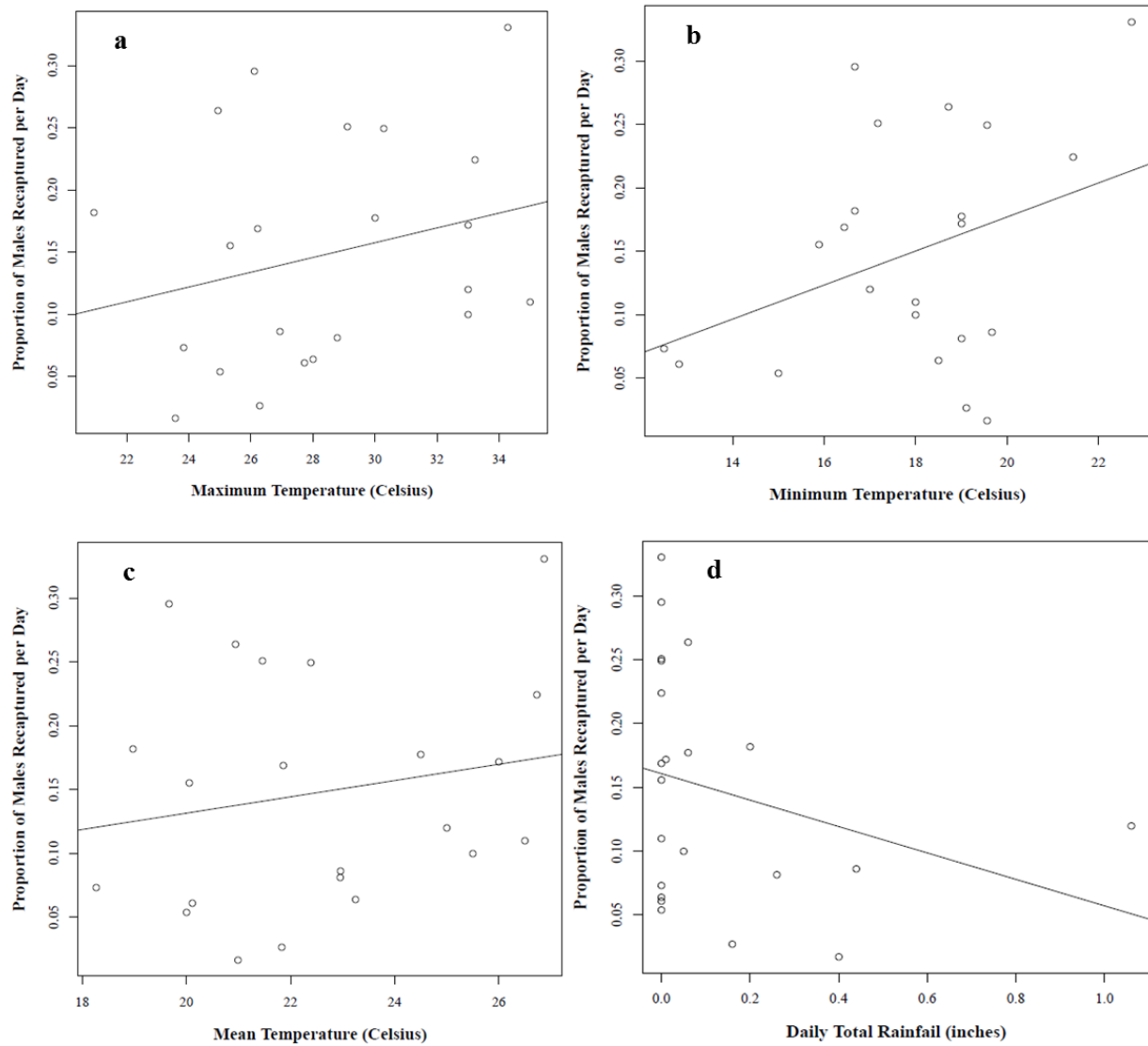


Figure 4. Comparison of weather variables and the proportion of males recaptured on a specific day. a) Maximum daily temperature in °C. b) Minimum daily temperature in °C. c) Mean daily temperature in °C. d) Total daily rainfall in inches. None of the relationships were significant ($p > 0.05$).

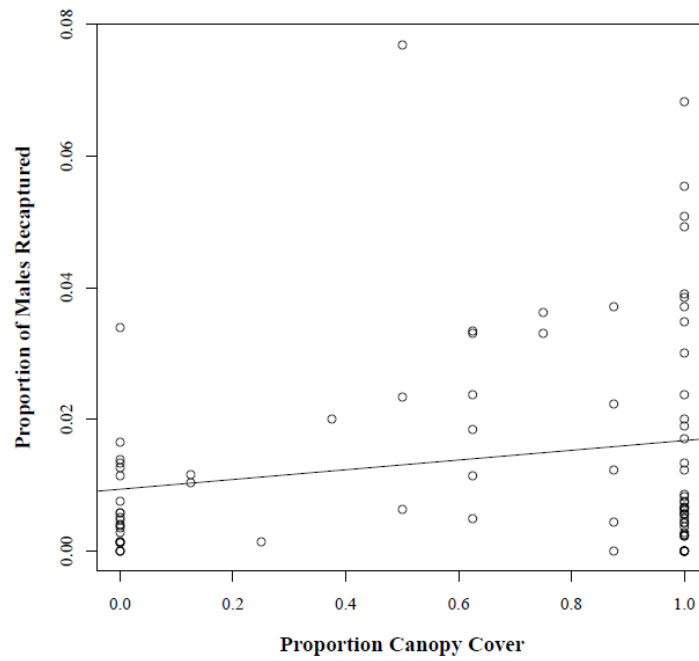


Figure 5. The positive relationship between proportion canopy cover and the proportion of males recaptured over the course of the experiment in a given trap location. The relationship is marginally significant ($R^2_{\text{adj}} = 0.027$, $F_{1, 82} = 3.269$, $p = 0.074$).

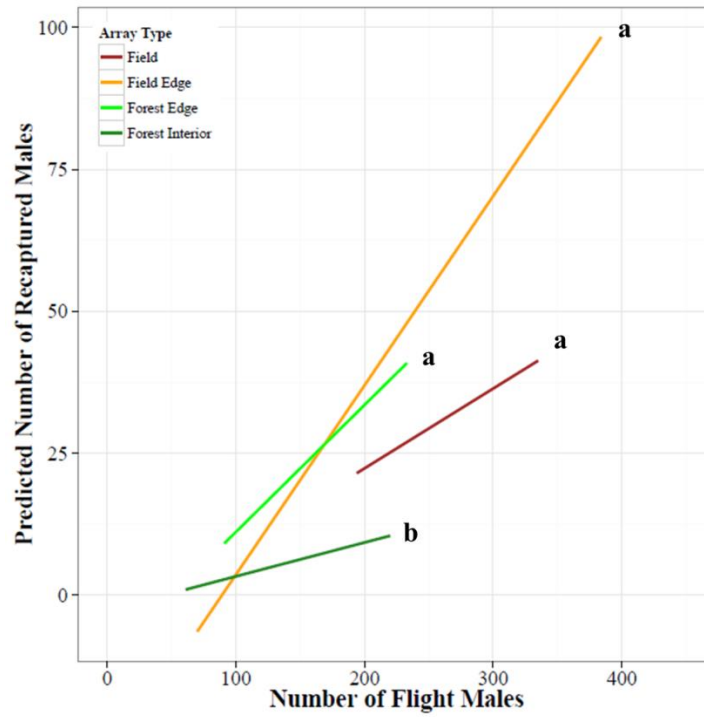


Figure 6. Comparison among array types. Data was analyzed using number of males recaptured as a function of array type, flight males, and females per trap in a generalized linear mixed effects model with site and day as random effects. The line graph shows the predicted number of recaptured males per array type across all releases based on the number of flight males. Different letters denote a significant ($p < 0.05$) difference.

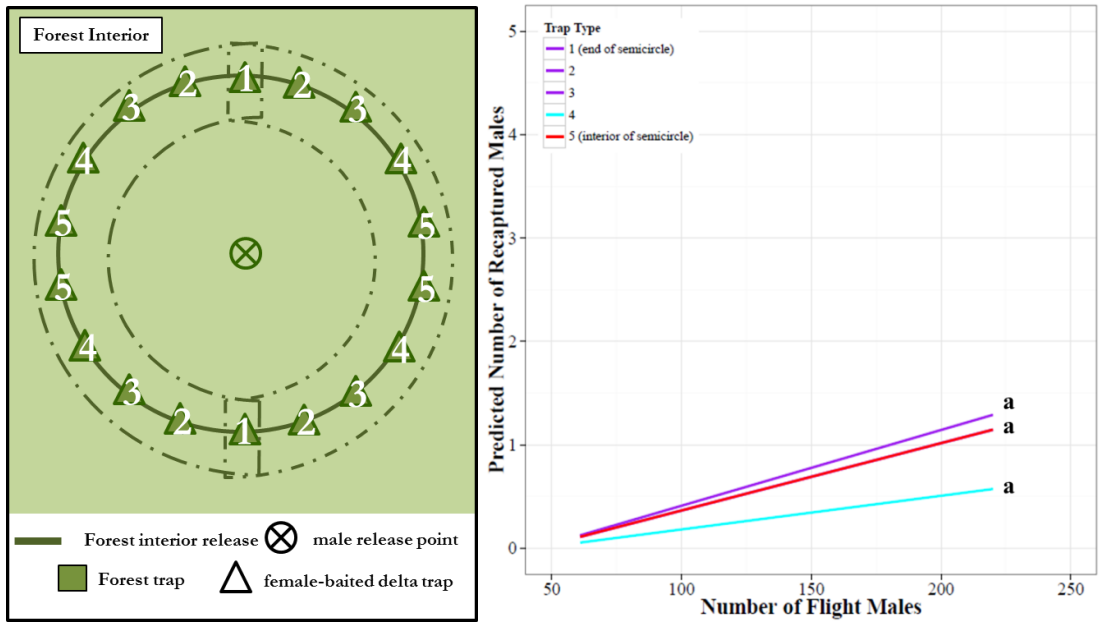


Figure 7. Forest array comparison of trap types. Data was analyzed using number of males recaptured as a function of trap type, flight males, and females per trap in a generalized linear mixed effects model with site and day as random effects. The line graph shows the predicted number of recaptured males per trap type across all releases based on the number of flight males. Trap types 1, 2, and 3 estimates are overlapping; therefore, they are depicted using one line on the graph. Different letters denote a significant ($p < 0.05$) difference.

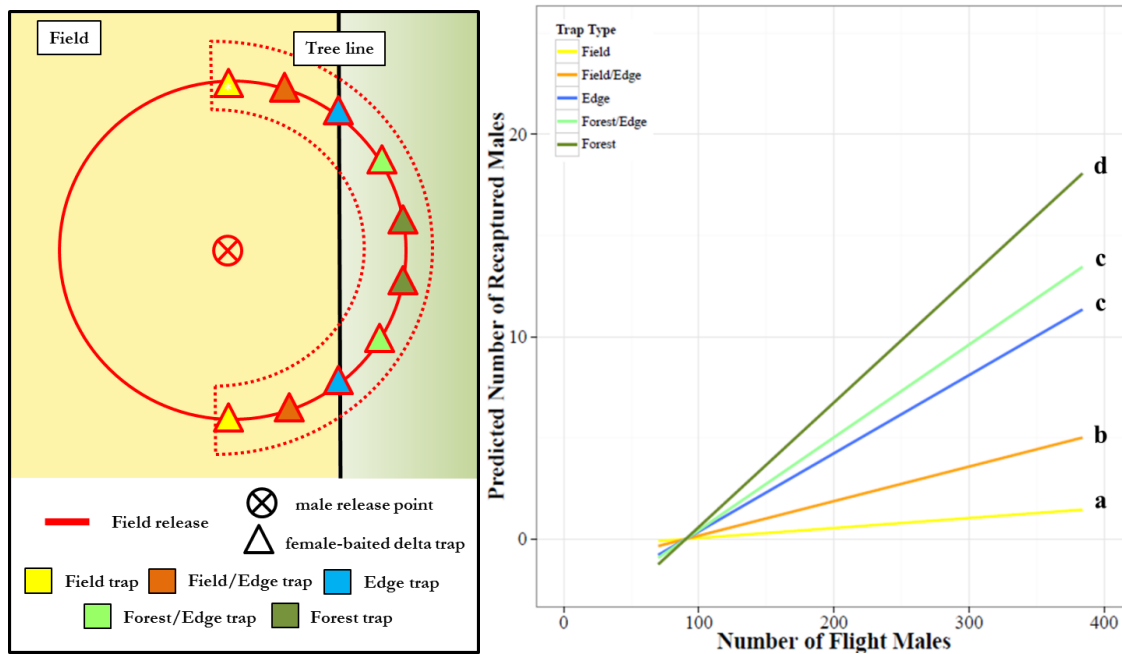


Figure 8. Field edge array comparison of trap types. Data was analyzed using number of males recaptured as a function of flight males and trap type in a generalized linear mixed effects model with site and day as random effects. The line graph shows the predicted number of recaptured males per trap type across all releases based on the number of flight males. Different letters denote a significant ($p < 0.05$) difference.

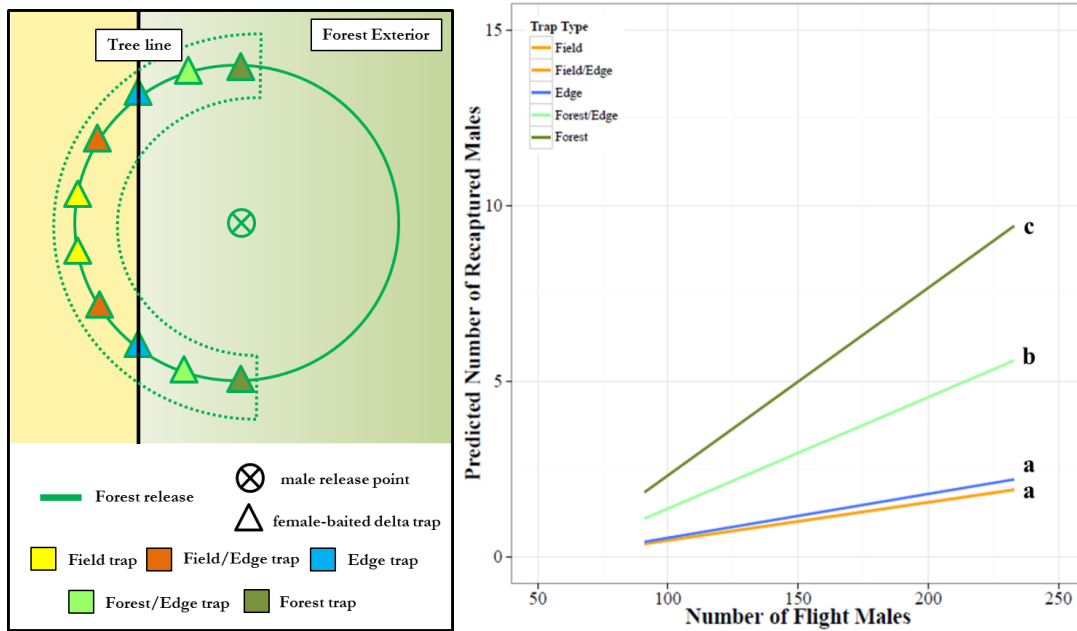


Figure 9. Forest edge array comparison of trap types. Data was analyzed using number of males recaptured as a function of trap type and flight males in a generalized linear mixed effects model with site and day as random effects. The line graph shows the predicted number of recaptured males per trap type across all releases based on the number of flight males. Field and Field/Edge traps had overlapping estimates; therefore, they are shown as one line in the graph. Different letters denote a significant ($p < 0.05$) difference.

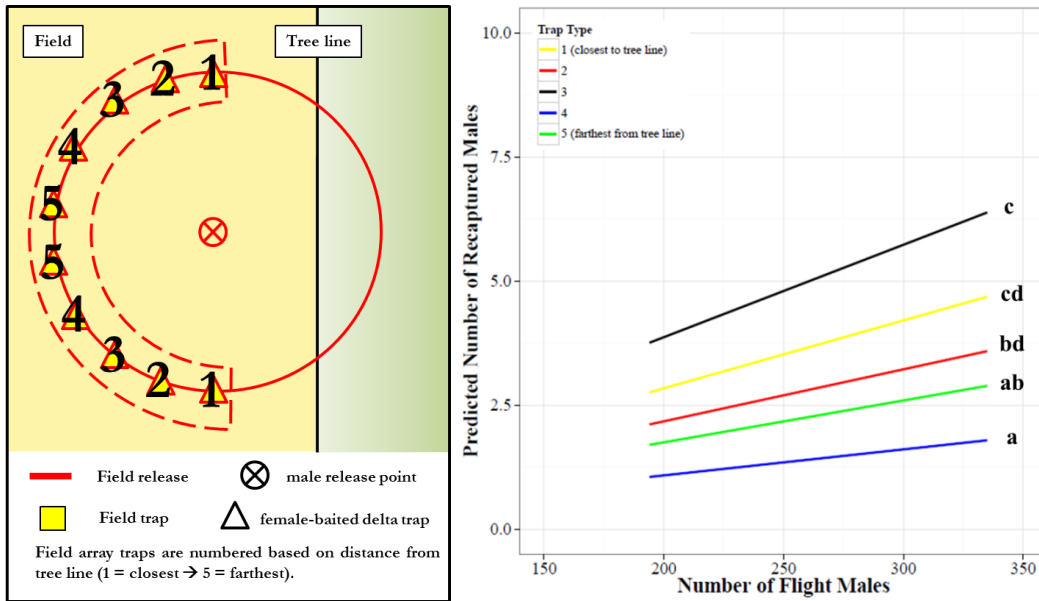


Figure 10. Field array comparison of trap types. Data was analyzed using number of males recaptured as a function of trap location, flight males, and females per trap in a generalized linear mixed effects model with site and day as random effects. The line graph shows the predicted number of recaptured males per trap type across all releases based on the number of flight males. Different letters denote a significant ($p < 0.05$) difference.

LITERATURE CITED

LITERATURE CITED

- Aars, J., & Ims, R. (2000). Population Dynamic and Genetic Consequences of Spatial Density-Dependent Dispersal in Patchy Populations. *The American Naturalist*, 155(2), 252–265.
- Bascompte, J., & Sole, R. V. (1996). Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology*, 65(4), 465–473.
- Bellinger, R. G., Ravlin, F. W., & McManus, M. L. (1989). Forest edge effects and their influence on gypsy moth (Lepidoptera: Lymantriidae) egg mass distribution. *Environmental Entomology*, 18(5), 840–843.
- Bender, D., & Fahrig, L. (2005). Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology*, 86(4), 1023–1033.
- Campbell, R. W., Miller, M. G., Duda, E. J., Biazak, C. E., & Sloan, R. J. (1976). Man's Activities and Subsequent Gypsy Moth Egg-mass Density Along the Forest Edge. *Environmental Entomology*, 5(2), 273–276.
- Charlton, R. E., & Cardé, R. T. (1990). Orientation of male gypsy moths, *Lymantria Dispar* (L.), to pheromone sources: The role of olfactory and visual cues. *Journal of Insect Behavior*, 3(4), 443–469.
- Contarini, M., Onufrieva, K. S., Thorpe, K. W., Raffa, K. F., & Tobin, P. C. (2009). Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. *Entomologia Experimentalis et Applicata*, 133(3), 307–314.
- David, C. T., Kennedy, J. S., & Ludlow, A. R. (1983). Finding of a sex pheromone source by gypsy moths released in the field. *Nature*, 303, 804–806.
- Doane, C.C. (1968). Aspects of mating behavior of the gypsy moth. *Annals of the Entomological Society of America*, 61 (3), 768-773.
- Dover, J., & Settele, J. (2009). The influences of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation*, 13(1), 3–27.
- Elkinton, J. S., & Liebhold, A. M. (1990). Population dynamics of gypsy moth in North America. *Annual Review of Entomology*, 35, 571–596.

- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515.
- Haddad, N. M., & Tewksbury, J. J. (2005). Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications*, 15(1), 250–257.
- Harrison, K. A., Pavlova, A., Amos, J. N., Takeuchi, N., Lill, A., Radford, J. Q., & Sunnucks, P. (2013). Disrupted fine-scale population processes in fragmented landscapes despite large-scale genetic connectivity for a widespread and common cooperative breeder: the superb fairy-wren (*Malurus cyaneus*). *The Journal of Animal Ecology*, 82(2), 322–33.
- Haynes, K. J., & Cronin, J. T. (2006). Interpatch movement and edge effects : the role of behavioral responses to the landscape matrix. *Oikos*, 113(1), 23–54.
- Haynes, K. J., Liebhold, A. M., Fearer, T. M., Wang, G., Norman, G. W., & Johnson, D. M. (2009). Spatial synchrony propagates through a forest food web via consumer–resource interactions. *Ecology*, 90(11), 2974–2983.
- Laurance, W. F., Pérez-Salicrup, D., Delamônica, P., Fearnside, P. M., D'Angelo, S., Jerozolinski, A., Lovejoy, T. E. (2001). Rain Forest Fragmentation and the Structure of Amazonian Liana Communities. *Ecology*, 82(1), 105–116.
- Leonard, D.E. (1981). Bioecology of the Gypsy Moth. In C.C. Doane & M.L. McManus (Eds.), *The Gypsy Moth: Research toward Integrated Pest Management* (pp. 9-29). USDA: Forest Service Tech. Bull. 1584.
- MacArthur, R.H. & Wilson E.O. 1967. The theory of island biogeography. Princeton, Univ. Press.
- Mastro, V.C. (1981). Evaluation of Disparlure-Baited Traps. In C.C. Doane & M.L. McManus (Eds.), *The Gypsy Moth: Research toward Integrated Pest Management* (pp. 549-554). USDA: Forest Service Tech. Bull. 1584.
- Menéndez, R., Gutiérrez, D., & Thomas, C. D. (2002). Migration and Allee effects in the six-spot burnet moth *Zygaena filipendulae*. *Ecological Entomology*, 27, 317–325.
- Murlis, J., Willis, M. A., & Cardé, R. T. (2000). Spatial and temporal structures of pheromone plumes in fields and forests. *Physiological Entomology*, 25, 211–222.
- Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44(1), 50–59.
- Ries, L., & Sisk, T. D. (2004). A Predictive Model of Edge Effects. *Ecology*, 85(11), 2917–2926.
- Sharov, A., & Liebhold, A. (1998). Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications*, 8(4), 1170–1179.

- Stephens, S. E., Koons, D. N., Rotella, J. J., & Willey, D. W. (2003). Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biological Conservation*, *115*(1), 101–110.
- Thomas, J. A., Bourn, N. A. D., Clarke, R. T., Stewart, K. E., Simcox, D. J., Pearman, G. S., ... Goodger, B. (2001). The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society London Biological Sciences*, *268*(1478), 1791–6.
- Tobin, P. C., Whitmire, S. L., Johnson, D. M., Bjørnstad, O. N., & Liebhold, A. M. (2007). Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecology Letters*, *10*, 36–43.
- Unfried, T. M., Hauser, L., & Marzluff, J. M. (2012). Effects of urbanization on Song Sparrow (*Melospiza melodia*) population connectivity. *Conservation Genetics*, *14*(1), 41–53.
- Vandermeer, J., Hoffman, B., Krantz-Ryan, S. L., Wijayratne, U., Buff, J., & Franciscus, V. (2001). Effect of Habitat Fragmentation on Gypsy Moth (*Lymantria dispar* L.) Dispersal: The Quality of the Matrix. *The American Midland Naturalist*, *145*(1), 188–193.
- Wiens, J. A., Crawford, C. S., & Gosz, J. R. (1985). Boundary dynamics : A conceptual framework for studying landscape ecosystems. *Oikos*, *45*(3), 421–427.
- Wiens, J. A., Stenseth, N. C., Van Horne, B., & Ims, R. A. (1993). Ecological Mechanisms and Landscape Ecology. *Oikos*, *66*(3), 369–380.
- Willis, M. A., David, C. T., Murlis, J., & Cardé, R. T. (1994). Effects of Pheromone Plume Structure and Visual Stimuli on the Pheromone-Modulated Upwind Flight of Male Gypsy Moths (*Lymantria dispar*) in a Forest. *Journal of Insect Behavior*, *7*(3), 385–409.

APPENDIX

Table 1. Male recapture data by day of release and trap array

Site	Array Type	Day of release (day of year)	Number of females/trap	Number of males released	Number of non-flight males	Number of flight males	Total number of males recaptured
Forest	Forest interior	205	1	158	0	158	10
Forest	Forest interior	215	2	205	0	205	5
Forest	Forest interior	212	1	62	1	61	1
Forest	Forest interior	217	2	220	0	220	16
Forest	Forest interior	219	2	189	0	189	5
Horse	Forest edge	169	2	201	3	198	17
Horse	Forest edge	177	2	121	0	121	12
Horse	Forest edge	213	2	91	0	91	6
Soybean	Forest edge	170	2	233	0	233	58
Soybean	Forest edge	213	2	91	0	91	18
Soybean	Forest edge	215	2	205	1	204	32
Horse	Field edge	171	2	297	2	295	87
Horse	Field edge	176	2	165	10	155	17
Horse	Field edge	179	2	270	2	268	32
Soybean	Field edge	175	2	192	122	70	12
Soybean	Field edge	200	2	477	93	384	127
Soybean	Field edge	208	2	283	10	273	46
Cow	Field edge	178	2	306	7	299	53
Horse	Field	201	2	222	12	210	47
Horse	Field	207	1	283	19	264	16
Horse	Field	209	1	203	5	198	16
Horse	Field	214	2	202	8	194	37
Soybean	Field	206	1	261	0	261	14
Soybean	Field	214	2	202	1	201	12
Soybean	Field	216	2	335	0	335	52

VITA

Lily M. Thompson was born in Louisville, Kentucky, USA on September 22, 1988. She graduated from duPont Manual High School and the Youth Performing Arts School in Louisville, Kentucky in 2006. She went on to receive her Bachelor of Science *cum laude* in Biology and Music from Centre College in Danville, Kentucky in 2010. In 2008, Lily studied abroad at the University of Reading in Reading, England. She spent two years collecting ecological monitoring data with the Student Conservation Association and the University of Tennessee-Knoxville before entering Virginia Commonwealth University's Biology Master's program in fall of 2012. While at Virginia Commonwealth University she has taught eight sections of Introduction to Biology Lab (BIOZ 151) as a graduate teaching assistant and was the secretary for the Graduate Organization of Biology Students (2013-2014). She will complete the post-baccalaureate certificate program in geographic information systems from Virginia Commonwealth University in May 2014.