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**Indirect effects between deer, mice, and the gypsy moth in a forest community**

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

By

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May 2014

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## **ABSTRACT**

### **INDIRECT EFFECTS BETWEEN DEER, MICE, AND THE GYPSY MOTH IN A FOREST COMMUNITY**

By John Wojcikiewicz, 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

White-tailed deer are ecosystem engineers that dramatically alter forest understory vegetation. Consequently, deer can impact many species in a forest through both direct and indirect effects. One species that deer may indirectly affect is the gypsy moth, whose pupae are preyed upon by the white-footed mouse. Through alterations to understory habitat of mice, deer may reduce mouse predation on gypsy moth pupae. In this study, I tested for indirect effects of deer on the gypsy moth by comparing mouse abundance, vegetation properties, and predation on pupae inside, and outside, of long-term deer exclosures. Overall, I did not find evidence for indirect effects of deer on the gypsy moth. There was little effect of the exclosures on mouse abundance, predation rates, and habitat measures. High mouse abundances, which likely resulted from a large acorn mast the previous year, may be obscuring indirect effects that would be detected at lower mouse abundances.



## INTRODUCTION

In classic predation studies, predator-prey relationships have often been considered as pairwise interactions isolated from extrinsic influences. However, interactions with a third species, such as through resource competition or habitat alteration can significantly alter predator-prey outcomes (Schmitz et al. 2004), and are termed *indirect effects* (Abrams 1995, Abrams et al. 1996, Werner and Anholt 1996). Accounting for indirect effects is vital to understanding many community-level interactions, especially when a species with far-reaching ecological impacts is involved.

In the forests of North America, white-tailed deer (*Odocoileus virginianus*) act as ecosystem engineers that can dramatically alter the structure and composition of understory vegetation. Ecosystem engineers modify the physical structure of their environment to an extent that can restructure entire ecological communities (Jones et al. 1994, 1997, Wilby et al. 2000, Baiser et al. 2008). The most apparent way that deer alter forest vegetation is through herbivory, although multiple other trophic interactions and modifications of abiotic resources have been attributed to deer (McShea and Rappole 1992, Rooney and Waller 2003, Cote et al. 2004). While many studies have investigated direct effects between deer and other forest species, few studies have examined species that deer may indirectly affect. One such species is the European gypsy moth (*Lymantria dispar*),

which deer may indirectly affect via trophic interactions with an important natural enemy of the moth.

The gypsy moth is an invasive forest defoliator that was introduced in New England in 1869 and has spread across the majority of the Eastern United States. A diverse array of natural enemies attack the gypsy moth across its U.S. range including infectious pathogens, parasitic insects, and a suite of invertebrate and vertebrate generalist predators (Elkinton and Liebhold 1990). These natural enemies attack the moth primarily during immature stages (Doane and McManus 1981) and are considered to be a major driver of gypsy moth population dynamics in the United States (Elkinton and Liebhold 1990).

The gypsy moth exhibits regional cyclical population outbreaks and crashes, usually with multiple low-density years between outbreaks. At peaks in population density, gypsy moths defoliate large tracts of forest, causing significant ecological and economic damage across its expanding range in the United States. During a gypsy moth outbreak, the combined effects of an introduced fungal pathogen (*Entomophaga maimaiga*) and infection from the nuclear polyhedrosis virus on late instar larvae likely causes the population to crash (Elkinton and Liebhold 1990). In contrast, generalist predators have little effect on high-density gypsy moth populations. This is largely due to the fact that generalists consume multiple species, often resulting in little or no numerical response to changes in the abundance of one prey item (Hanski 1990).

Predators do have relatively strong effects on low-density population dynamics of the gypsy moth. A suite of generalist predators acting on later (5<sup>th</sup> and 6<sup>th</sup>) instar larvae and pupae are responsible for the majority of mortality among low-density gypsy moth populations. Avian, invertebrate, and small mammal predation on the gypsy moth have all

been documented, and at least 7 species of invertebrate parasitoids have been described infecting North American gypsy moth populations (Elkinton and Liebhold 1990).

In Eastern North America, the white-footed mouse (*Peromyscus leucopus*; hereafter referred to as mice) is the dominant source of gypsy moth mortality during non-outbreak periods (Elkinton et al. 1996, Ostfeld et al. 1996, Jones et al. 1998). Mice are ubiquitous in forests throughout the gypsy moth's range, and include the pupae in their diet. The consumption rate of pupae increases linearly with mouse density, and such predation has been implicated as a significant factor in the suppression of low-density gypsy moth populations (Elkinton et al. 1996 Ostfeld et al. 1996, Jones et al. 1998). However, mouse populations do not show a numerical response to increased gypsy moth density (Soloman 1949, Schauber et al. 2004), which is likely a result of gypsy moth pupae being present for only a few weeks in the summer when other food sources are abundant (Elkinton and Leibhold 1990).

With regard to predation rate, mice show a type II or a weak type III functional response to the density of gypsy moth pupae, neither of which have been found to effectively regulate gypsy moth populations around a low density threshold (Elkinton et al. 1996, Elkinton et al. 2004, Schauber et al. 2004). However, because the population dynamics of mice and the gypsy moth are decoupled, sufficiently high mouse population densities can effectively suppress low-density gypsy moth populations (Elkinton 1996, Jones et al. 1998, Gschwanter et al. 2002, Schauber et al. 2004). Therefore, identifying the factors that drive the population dynamics of mice is imperative to understanding their potential ability to suppress gypsy moth populations and possibly prevent outbreaks.

Season-to-season mouse populations are regulated by their reliance on acorn storage for over-winter survival. Mouse density in the early summer is strongly correlated with oak masts from the previous autumn (Elkinton et al. 1996, Ostfeld et al. 1996, Jones et al. 1998), and it has been suggested that periods of low acorn density will release gypsy moth populations from predation due to reductions in small mammal density (Ostfeld et al. 1996, Jones et al. 1998, Liebhold et al. 2000). Furthermore, oak trees often mast synchronously at a regional scale, which appears to drive the synchronization of mouse and gypsy moth populations at a similar spatial scale (Haynes et al. 2009). Oak masts are therefore an important indirect causal factor for gypsy moth predation.

In addition to oak masting, the white-tailed deer may affect the population densities and distributions of mice within a forest ecosystem. Densities of these ecosystem engineers in the eastern U.S. are thought to be 2 to 4 times higher than before pre-European settlement (Alverson and Waller 1988). Deer are voracious consumers of acorns (McShea and Rappole 1992) and during the fall, will move into oak hickory stands where they consume up to 67% of the available acorn crop (McShea and Schwede 1993). Competition for acorns between deer and mice, especially during low mast years, may reduce mouse densities the following spring due to insufficient over-winter acorn storage.

Furthermore, deer significantly alter the understory vegetation structure of the forest by consuming herbs, shrubs, and seedlings, and altering patterns of succession. Deer density and exclosure studies have found reductions in stem density of tree seedlings and some shrub species, reduced herb cover, reduced seedling recruitment and decreased species richness of understory species in the presence of deer (Flowerdew and Elwood 2001, Russell et al. 2001).

The structural and compositional alteration of understory vegetation by deer may impact within-season mouse populations in multiple ways. Many species of small mammal including the white-footed mouse strongly prefer patches of dense, shrubby understory vegetation for foraging, nest building and predator avoidance (Dueser and Shugart 1978, Putnam et al. 1989). Within a forest ecosystem, mice show a positive numerical response to increased shrub density and forb cover and will aggregate in patches of high-density vegetation (M'Closkey 1975, M'Closkey and Lajoie 1975, Dueser and Shugart 1978). Habitat complexity with regards to understory species composition and structural variation are also positively correlated with mouse density (Carey and Harrington 2001, Anderson et al. 2003).

Taken together, there exist multiple pathways by which deer may impact mice. However, few studies have quantitatively investigated interactions between deer, mice, and gypsy moths. One challenge in conducting such studies is finding study sites with consistently different densities of deer between treatments, or areas from which deer have been completely excluded for significant period of time (Russell et al. 2001). Furthermore, deer, small mammals, and the gypsy moth are components in a complex system of linkages (Figure 1), from which it is a challenge to parse out individual pairwise interactions. Many studies have addressed the role of acorns in this system and shown that variation in year-to-year acorn masts can release low-density gypsy moth populations from predation due to the reliance of mice on acorns for over-winter survival (Elkinton et al. 1996, Ostfeld et al. 1996, Jones et al. 1998). However, whether or not mice and their predation rates on gypsy moth pupae show a numerical response to deer activity remains unclear. Resolving such a response would greatly increase the understanding of the ability of mice to maintain low-

density populations of gypsy moth through predation, and implicate deer as a key player in that process.

This study utilized long-term deer exclosures in a mature oak-hickory forest to test for effects of deer on predation of gypsy moth pupae by mice. Mouse abundances and vegetation properties were also compared between exclosures and controls. I predicted that mouse abundances would be greater in the exclosures due to better quality habitat and/or a lack of competition for acorns with deer, and this would result in higher predation on gypsy moth pupae by mice in the exclosures.

## METHODS

*Study Area:* The two deer exclosure sites were both located in the north section of Shenandoah National Park (SNP), within 5 km of the Mathew's Arm campground (38°45'50"N, 78°17'33"W). Site one (Mathew's Arm) was within 500m of the campground and site two (Keyser) was located 5 km NE of Mathew's Arm. Both sites were composed primarily of mature oak (*Quercus sp.*), hickory (*Carya sp.*), white ash (*Fraxinus americana*), and tulip poplar (*Liriodendron tulipifera*). The dominant understory shrubs at both sites were *Cornus florida*, *Lindera benzoin*, *Cercis canadensis* and *Hamamelis virginiana*.

The deer exclosures were erected in early 1991, and are composed of high tensile wire with 25 X 25 cm mesh farm fencing at the bottom (McShea 2000). At 3m high, the fencing successfully excludes deer, but not small and medium vertebrates (Leimgruber et al. 1994). Both exclosures are 4 ha in area. Each exclosure was paired with an identically

sized control treatment that was within 20m of the side of the enclosure. Deer density at these sites is consistently above 25 deer/km<sup>2</sup> (McShea, pers. comm.).

*Small mammal trapping:* Small mammal trapping was conducted at each site during three trapping sessions over the summer of 2013. Session one occurred from 6/11 to 6/15, session two from 7/8 to 7/12, and session three from 7/22 to 7/26. Each trapping session consisted of one day of pre-baiting followed by 3 days (72 h) of trapping. The traps were set each evening and checked after sunrise the following morning. Captured individuals were marked with a unique ear tag, sexed, checked for ticks, and released. A mixture of sunflower seeds, rolled oats, and cracked corn was used to bait the traps.

At each site, one Sherman trap (Sherman Trap Company, Tallahassee, Florida) was placed every 10m along 50m transects in both the enclosure and control treatments. Transects were spaced 10m apart. At the Mathew's arm treatments (MA.E. and MA.C.), there were five transects for a total of twenty-five traps (0.25 ha). At Keyser (K.E. and K.C.), there were six transects for a total of thirty traps (0.30 ha). In the enclosures, all transects were positioned such that no traps were located within 20m of the fence.

*Predation on gypsy moth pupae:* Predation rates on gypsy moth pupae were measured by deploying live gypsy moth pupae along transects in the enclosure and control treatments at both sites. Although, the gypsy moth has been present in Shenandoah National Park since the early 1990's, irradiated (non-viable) pupae were deployed so as not to augment the natural moth population. The transects that were established for the small mammal trapping were utilized for this portion of the study. One pupa was placed on a 4 X 4 inch square of burlap on the forest floor every 10m along each transect. At each site and for each sampling session, five of the pupae were placed on track plates in order to detect

footprints of potential pupae predators. The track plates were constructed by spreading a mixture of graphite powder, alcohol, and mineral oil over acetate sheets as per Connors et al. (2005).

There were three pupae predation sampling sessions over the summer of 2013. Session one occurred from 6/25 to 6/28, session two from 7/16 to 7/19, and session three from 7/29 to 8/2. Each session was three days in length. During the first day, the burlap squares and track plates were placed on the forest floor with no pupae on top to allow the animals to acclimatize to their presence. On day two, one pupa was placed on each burlap square/track plate. Each pupa was then checked the next morning to determine if predation had occurred. Predated pupae were replaced and then checked again the following morning. Upon checking the pupae after deployment, multiple factors were used to identify the predator. Some pupae were completely removed from the burlap/track plates, but most were predated where they were found, leaving the pupal casing behind. The hallmarks of white-footed mouse predation are large fragments of pupal casing with jagged edges that result from the incisors (Hastings et al. 2002). Furthermore, because consuming the pupae requires a significant handling time, easily identifiable feces were left on the burlap/track plates in almost all instances of predation. Finally, footprints left on the track plates were used to identify predators.

*Vegetation Analysis:* Understory habitat properties at each site were measured using visual percent cover estimates and the identification of the dominant shrub and forb species. For consistency, I performed all percent cover estimates. A 5m radius was centered on each point along every small-mammal trapping/predation transect. Each radius was then divided into four quadrants. Within each quadrant, percent cover estimates were



made at the ground, mid, and canopy layer. At the ground layer, measures included leaf litter, downed woody debris, rocks, soil, and forb. For the mid layer, estimates were made for shrubs and seedlings. Finally, percent canopy cover was estimated. At each point, the percent cover estimates from the four quadrants were averaged together to obtain a value for each measure.

*Statistical Analysis:* The numbers of small mammals captured from each session were calculated using the minimum number alive (MNA) method (Krebs 1966). Values obtained from the MNA method are based only on the minimum number of individuals known to be alive at a given time, and do not include any population inferences. In order to obtain small mammal abundance estimates that include population inferences, the mark-recapture data was analyzed using Pollock's Robust Design Model (Pollock 1982) implemented in Program MARK. With this method, it was assumed that populations were closed to birth, death, emigration and immigration within trapping sessions but open to these events between trapping sessions. Model averaging was utilized so that each abundance estimate is a weighted average from all of the models constructed in MARK.

One-way ANOVA was utilized to test for the effect of time (sampling session) on predation rate for each treatment. In order to test for the presence of a behavioral response from the mice to the repeated deployment of pupae, t-tests were used to compare the proportion of pupae predated between consecutive days within each sampling session. A generalized linear mixed effects model was constructed to assess the effect of treatment (control or enclosure) on predation, while treating time as a random effect. Differences among sites with respect to measures of understory habitat were compared using one-way ANOVA.

Finally, a mixed-effects logistic regression model was constructed to fit the probability of predation on gypsy moth pupae as a response to habitat measures and small mammal abundance. The model included terms for treatment (control vs. enclosure), small mammal abundance, and the percent cover of forbs, shrubs, seedlings, canopy, leaf litter, rock, and woody debris. Site and sampling session (time) were treated as random effects. Unless otherwise stated, analyses were performed using R version 3.0.1 (R Foundation for Statistical Computing, Vienna, Austria).

## RESULTS

*Small mammal abundance:* There were 306 capture events during the study. Of these, 265 were white-footed mice (*Peromyscus leucopus*), 27 were meadow voles (*Microtus pennsylvanicus*), 9 were short-tailed shrews (*Blarina brevicauda*), and 5 were eastern chipmunks (*Tamias striatus*). A total of 117 individual *P. leucopus* were tagged, with a recapture rate of 44%. *P. leucopus* was by far the most trapped small mammal species in the forest understory at our sites.

Estimates of white-footed mouse abundance were obtained using program MARK (Figure 2). A black bear destroyed the majority of small mammal traps in the Mathew's Arm enclosure (MA.E.) treatment during sessions one and two. As a result, the unreasonably high abundance estimates obtained from these sessions were disregarded.

The estimates from MARK show very large standard errors at the Keyser control (K.C.) treatment for session two (Figure 2). This was the consequence of a much lower detection probability resulting from a majority of captures occurring on the last day of

trapping during that session at that site. The standard errors for all of the other MARK estimates were relatively low. The MNA calculations show a comparatively low count of small mammals known to be alive for site K.C. at trapping session two (Figure 3), which indicates that the actual abundance is likely in the lower half of the standard error range obtained from MARK. With the exception of site K.C. at trapping session two, the MARK estimates are likely more informative due to their inclusion of population inferences and low standard error.

Mouse abundance generally increased over the course of the season. However, based on the MARK estimates, the trend was not consistent for all of the sites. At treatments K.E. and possibly K.C., the highest abundances were observed during the second trapping period. At MA.C., mouse abundance increased consistently over the three sessions. A comparison between paired treatments (MA.E. – MA.C., K.E. – K.C.) reveals that mouse abundance was generally higher in the control plots than in the exclosures (Figure 2). This is true for all trapping sessions at the Keyser site, and for the one comparable estimate from the Mathew's Arm site. However, this relationship was not significant ( $p = 0.172$ ).

*Predation of gypsy moth pupae:* The predation rate on gypsy moth pupae increased significantly over the three sampling periods for both the control ( $F = 3.65$ ,  $df = 2$ ,  $p < 0.001$ ) and exclosure ( $F = 14.32$ ,  $df = 2$ ,  $p < 0.001$ ) sites (Figure 4). By sampling period three, the proportion of pupae predated was 0.97 at exclosure sites and 0.87 at control sites. The observed increase in predation rate over the summer is consistent with an increase in small mammal abundance.

There was little evidence of a behavioral response from the mice to the deployed pupae. Previous similar studies have found increases in predation on the second and third

consecutive days of sampling (Hastings et al. 2002), which is often attributed to the small mammals learning the location of the pupae. In this study, in only one out of the 12 sessions was the predation rate significantly higher on the 2<sup>nd</sup> sampling day.

In the mixed-effects model with sampling session (time) and treatment (control vs. exclosure) as independent variables, time had a significant effect on predation rate ( $F = 22.46$ ,  $df = 1$ ,  $p < 0.001$ ), but there was no significant treatment effect on predation rate ( $F = 1.54$ ,  $df = 2$ ,  $p = 0.2319$ ) (Table 2). There was a significant interaction effect between time and treatment ( $F = 6.19$ ,  $df = 2$ ,  $p = 0.009$ ). In the mixed-effects logistic regression model with habitat measures and small mammal abundance as independent variables, only percent shrub cover had a positive effect on predation ( $p = 0.021$ ). There was no significant relationship between predation and small mammal abundance ( $p = 0.3407$ ).

*Understory vegetation and habitat properties:* Percent cover estimates were made for forbs, shrubs, seedlings, leaf litter, soil, downed woody debris, and canopy cover at all sites. One-way ANOVA was utilized to test for differences in these measures between sites. The habitat measures that differed between control and exclosure treatments were not consistent between the two sites (Table 3). At the Mathew's Arm site, the exclosure had significantly higher ( $p = 0.004$ ) percent forb cover and significantly lower ( $p < 0.001$ ) seedling cover than the control. At the Keyser site, the exclosure plot had significantly lower ( $p = 0.013$ ) percent shrub cover and significantly higher ( $0.033$ ) canopy cover than the exclosure.

## DISCUSSION

The general increase in white-footed mouse abundance and predation rate on gypsy moth pupae observed in this study is consistent with population growth that occurs over the summer in temperate regions. Previous studies have shown that white-footed mouse abundance increases over the course of the summer (Rintamaa et al. 1976), especially following a large acorn mast in the previous fall (McShea and Schwede 1993, Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996, McShea 2000). A large acorn mast in autumn 2012 (McShea, pers. comm.) may explain why such high mouse abundance estimates were obtained during the summer of 2013.

White-footed mouse abundance did not increase consistently for all sites over the course of the study. From the MARK estimates (Figure 2), mouse abundance appeared to increase at a constant rate over time at site MA.C. At sites K.E and K.C, population abundances appear to peak at trapping session two (7/9 – 7/11) and then decrease at trapping session three (7/23 – 7/26). One possible explanation for the observed abundance patterns at K.E and K.C is that white-footed mice often exhibit bimodal reproductive activity, with peaks in reproductive output in spring and autumn and little activity in mid-summer (Jackson 1952, Rintamaa et al. 1976). In these studies, mouse populations were found to increase significantly from the first reproductive event until mid-summer, at which time populations declined until the second reproductive event in the autumn. It should be noted however that the pattern observed in this study is questionable because of a high standard error for one of the abundance estimates and some data was disregarded due to bear interference.

I did not find evidence that deer negatively affect mouse abundance in this study. In contrast, it appears that small mammal abundance was higher in the control plot than in the exclosure (Figure 2), although this relationship was not significant. This result is contrary to my prediction, as it was expected that small mammal abundances would be higher in the deer exclosures. I predicted that differences in the understory habitat between the control and exclosures would drive a difference in mouse abundance between the treatments. While some differences in habitat variables were detected between treatments, they were not consistent across sites, and may not have been large enough to drive a detectable difference in mouse abundance. It has been shown that that *P. leucopus* more intensively use local patches of understory vegetation with higher density and shrub cover (M'Closkey 1975, Dueser and Shugart 1978). However, *P. leucopus* is also a ubiquitous species in the understory, and is largely considered to be a habitat generalist (Dueser and Shugart 1978). When combined with high mouse abundances resulting from a large acorn mast, understory habitat alteration by deer may not elicit a numerical response in mouse abundance.

With respect to the predation rate on gypsy moth pupae, I predicted that predation would be higher in the exclosures than in the control plots, which was not observed. This result is consistent with the similar mouse abundances that were observed between the treatments. It should be noted that predation rates observed in this study were quite high. No sampling period had an average predation rate lower than 50%, and by the third sampling period nearly all deployed pupae were being consumed at every site (Figure 4). This is also likely a function of high mouse abundance. Previous studies that have examined small mammal predation on gypsy moth pupae observed lower predation rates or mouse

abundances than in this study (Campbell and Sloan 1977, Jones et al. 1998, Schauber et al. 2004). It is possible that such high abundances and predation rates may be obscuring a treatment effect that would be detected at lower mouse abundances.

I observed little consistency in the vegetation and habitat measures that differed between control and exclosure treatments (Table 3). The pattern of higher forb cover and lower seedling cover observed in the Mathew's Arm exclosure is consistent with preferential browsing on forbs by deer, which by reducing forb cover, may allow for higher rates of seedling establishment (Horsely and Marquis 1982). Furthermore, deer were observed browsing extensively on the dominant forb (*Laportea canasensis*), in the control plot (personal observation). The pattern of lower shrub cover and higher canopy cover observed at the Keyser exclosure is not as easily explainable. The higher percent canopy cover in the exclosure may be reducing the amount of shrub cover more dramatically than deer browsing does in the control plot. However, the lack of consistency between the two sites is still unexpected given that previous studies have attributed large reductions in the density of shrubs, seedlings, and forbs to deer browsing across a variety of habitats (Trumbell et al. 1989, Rooney 1997, Ritchie and Knops. 1998).

Despite the lack of consistency between paired treatments with respect to habitat variables, I did find evidence that shrub cover is a predictor of predation on gypsy moth pupae. This is consistent with previous findings that mice more intensively use shrubby patches of vegetation in a forest, which is likely due to the increased cover from predators that they afford (M'Closkey 1975). In this study, I did not find strong evidence that deer alter the percent cover of shrubs in the forest understory, which suggests that deer do not impact mice through alterations in the cover of important habitat properties.

The large acorn mast in the autumn of 2012 likely explains both the high abundance of mice and the very high predation rate on gypsy moth pupae observed in this study. These factors may be obscuring an effect of the deer exclosures that would be more detectable at lower mouse abundances. When a large acorn mast results in high mouse abundance, it is possible that local differences in habitat characteristics within a forest, some of which were observed in this study, become less important in determining the distribution of mouse populations at this scale (McShea 2000). Furthermore, competition for acorns is likely less intense when there is a large acorn mast, and resources are more plentiful.

This study corroborates previous findings that large acorn masts result in high predation rates on gypsy moth pupae the following year (Elkinton et al. 1996, Jones et al. 1998). However, the fact that both mouse abundance and the predation rate on gypsy pupae increases over the course of the season may highlight the importance of the timing of gypsy moth pupation in determining predation rate. It appears that the later in the season that gypsy moth pupation occurs, the higher the predation rate will be due to greater mouse abundances. The timing of gypsy moth pupation is largely a function of temperature, with lower temperatures resulting in later pupation times across the moth's range. However, future research is needed to determine if the variation in timing of gypsy moth pupation or mouse population growth within a season is great enough to have a significant impact on gypsy moth population dynamics.



## TABLES

Table 1. Minimum number alive calculations of small mammals at each site across the three trapping sessions.

Trapping Session	Site	Minimum Number Alive
1	MA.E	*
2	MA.E	*
3	MA.E	20
1	MA.C	13
2	MA.C	23
3	MA.C	23
1	K.E	6
2	K.E	22
3	K.E	17
1	K.C	7
2	K.C	13
3	K.C	27

\* Data excluded due to bear interference

Table 2. Results from the mixed effects model with time (sampling session) treated as a random effect

Effect	<i>df</i>	F-value	p-value
Sampling Session	2	22.46	< 0.001
Treatment	1	1.54	0.232
Sampling Session * Treatment	2	6.19	0.009

Table 3. Differences in the mean percent cover of habitat variables between treatments at each site

Compared Sites	Forb	Shrub	Seedling	Leaf Litter	Rock	Canopy
<b>MA.E - MA.C</b>	<b>12.4**</b>	<b>0.8</b>	<b>-15.2***</b>	<b>1.4</b>	<b>-3.4</b>	<b>1.6</b>
<b>K.E - K.C</b>	<b>-5.5</b>	<b>-8.0*</b>	<b>-5.3</b>	<b>0.5</b>	<b>-3</b>	<b>8.6*</b>
MA.E - K.E	25.8**	7.6*	10.7**	-5.7	4.9	-9.4*
MA.E - K.C	20.3***	-0.4	5.3	-5.2	1.9	-0.8
MA.C - K.E	13.4**	6.8	25.9***	-7.1	8.3*	-11.1**
MA.C - K.C	7.9	-1.2	20.5***	-6.6	5.3	-2.4

Bold text denotes paired treatments.

\* p-value < 0.05, \*\* p-value < 0.01, \*\*\* p-value < 0.001

## FIGURES

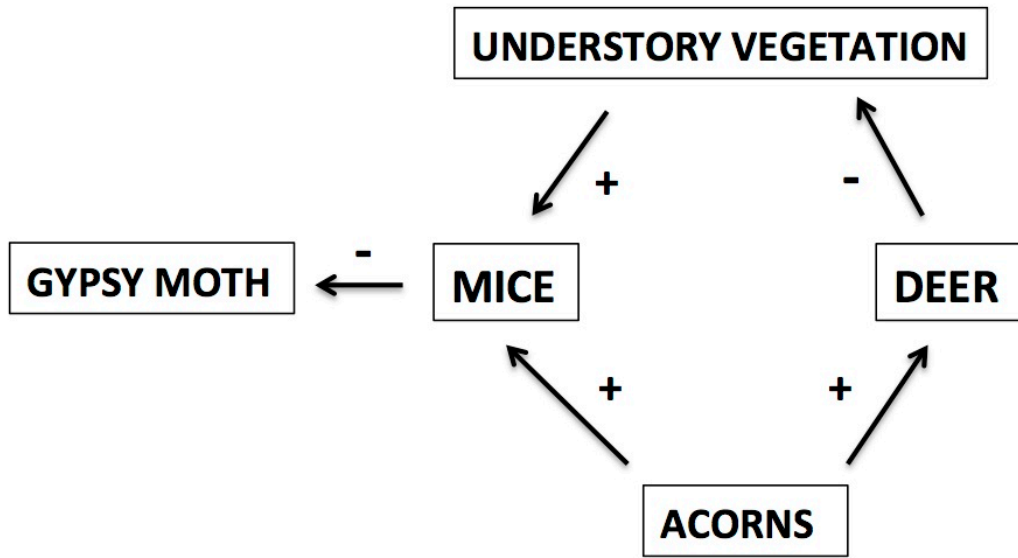


Figure 1. Hypothesized linkages and their direction (-,+ ) between acorns, deer, mice, understory vegetation and the gypsy moth within a forest community

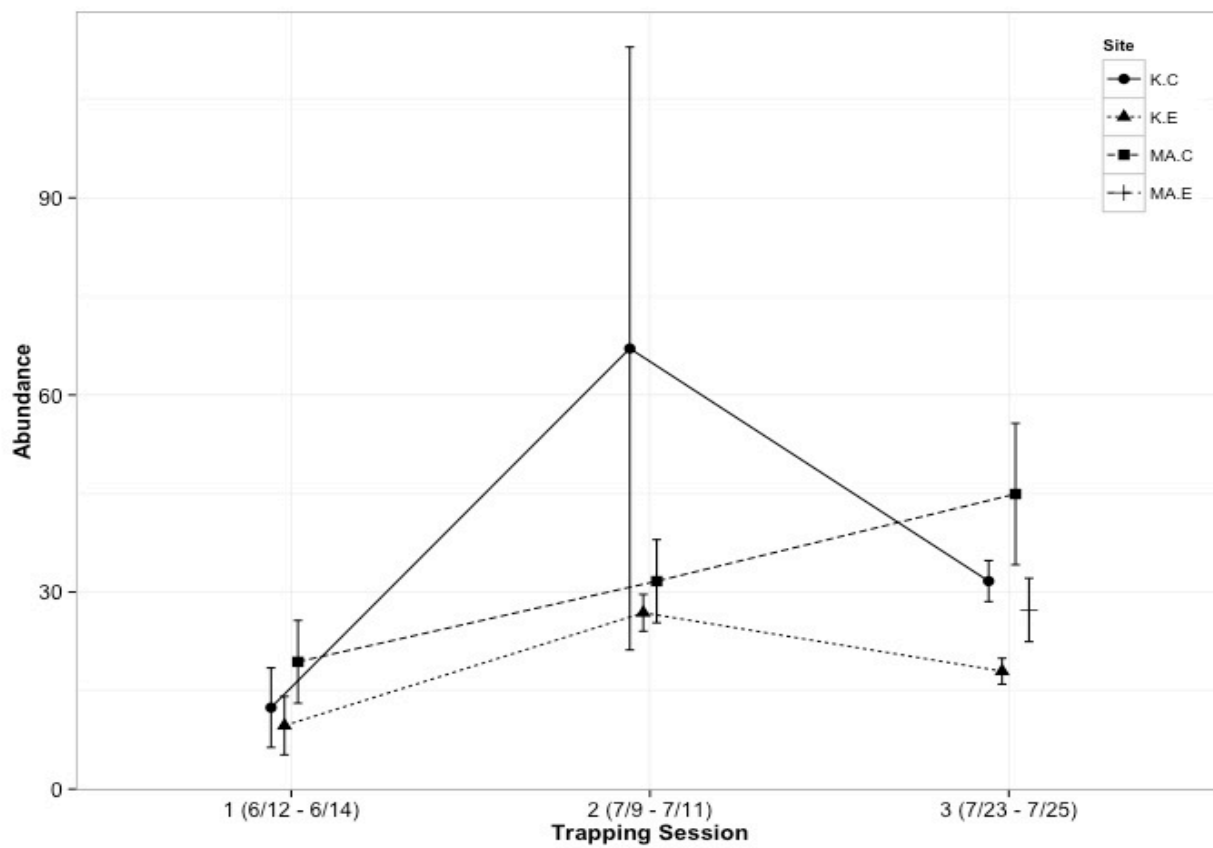


Figure 2. Changes in mouse abundance over the three trapping sessions at each site. Raw abundance estimates obtained from program MARK were used.

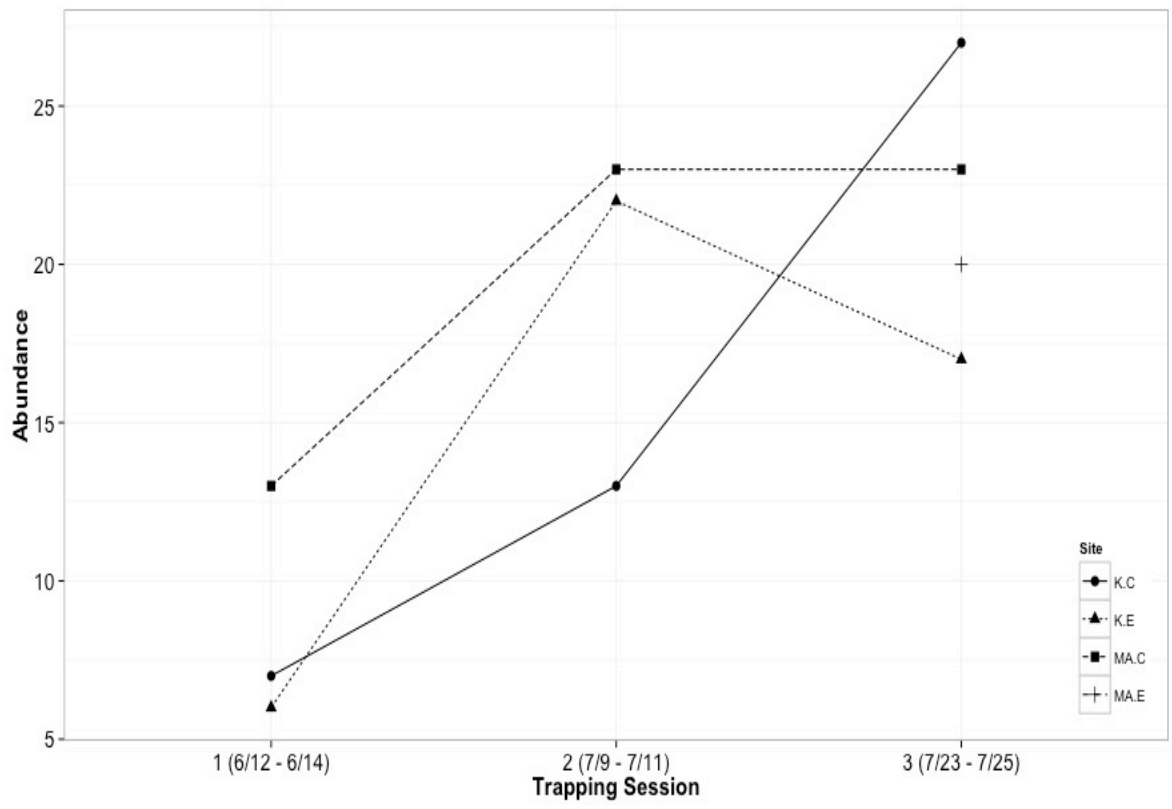


Figure 3. Changes in the minimum number of mice alive over the three trapping periods at each site.

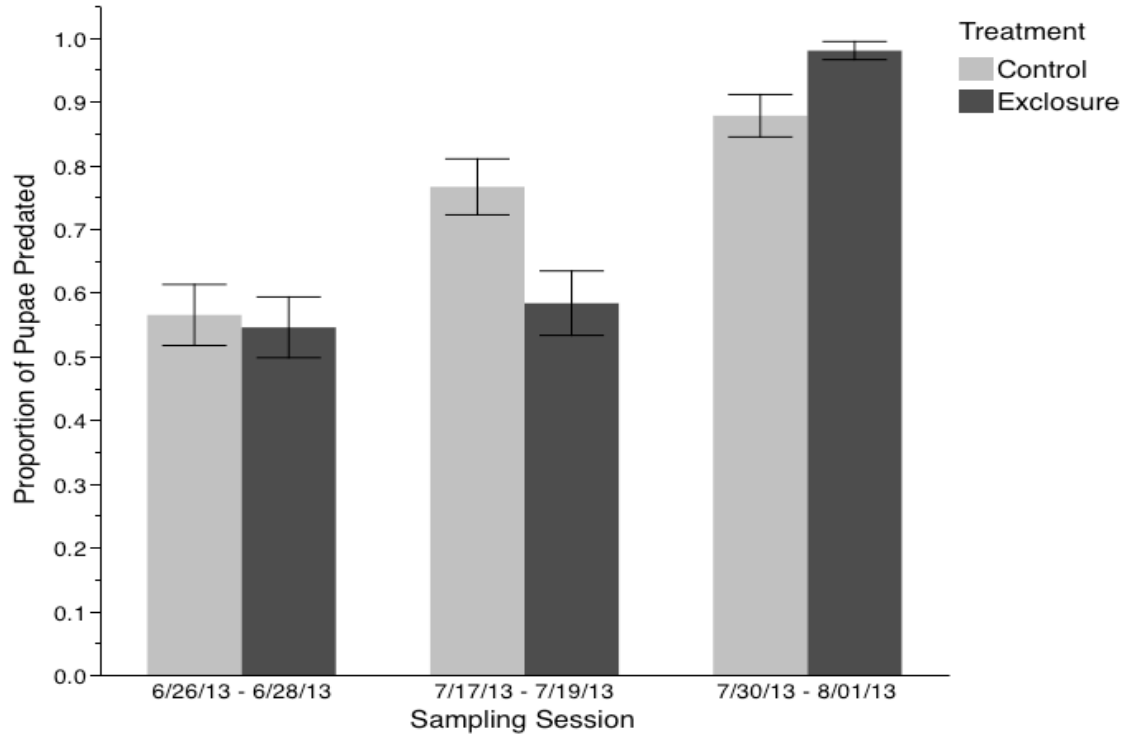


Figure 4. Predation on gypsy moth pupae in the control and exclosure treatments over the three sampling periods. Error bars denote standard errors.

**LITERATURE CITED**



## LITERATURE CITED

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