

# Understanding the population forcings of induced forest succession on *Peromyscus leucopus*

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## Abstract

As climate continues to shift across the globe, many forest ecosystems will succumb to the combined stress of temperature, precipitation, and biota shifts. In the spring of 2008, a group working at the University of Michigan Biological Station (UMBS) began an experiment to examine what may occur in the future. Housed near the UMBS AmeriFlux site, the Forest Accelerated Succession Experiment (FASET) artificially accelerated succession from an aspen-dominated hardwood forest to a conifer-deciduous mixed forest by girdling the overaged early-successional species, *Populus spp.* and *Betula papyrifera*. In order to understand the cascading trophic effects of FASET, we selected the *Peromyscus leucopus*, or white-footed mouse, as a preliminary study species. Population demographics are shifting within FASET, primarily when it relates to reproductive activity. Furthermore, early results indicate shifts in the importance of specific vegetation structure measures, specifically canopy openness and proximity of fine woody debris. As the manipulated forest continues to shift towards a deciduous-coniferous mixed forest, the subpopulation within FASET should continue adjusting to the new forest dynamic. It is my hope that trapping will continue in these areas to facilitate a deeper understanding of both *P. leucopus* behavioral and population changes in response to changing forests.

## Introduction

In recent years dialogues on climate change seem to be increasingly common in the public sphere, in part paralleling an increased acceptance of evidence of climatic warming. While all vary in context and focus, they all have a single common ground – apathy. Due to the temporal and spatial distances environmental problems encompass, we are often left with vague musings on slightly warmer winters. Unfortunately, the human mind is not built to deal with a problem of this scope because we are fundamentally irrational (Ariely 2009). Simply put, we are not mentally capable of, or most optimistically, highly averse to, motivating ourselves to change current lifestyles in order to buffer against negative consequences several years or decades down the line. Lack of political will within the United States shows the truth of such a statement. Given the state of current affairs, we are unlikely to see much progress from the general populace unless something gives.

Whereas long-term consequences cannot motivate change, immediate costs can. Rising temperatures not only function on a global scale but also alter small-scale regional dynamics as well (Karl *et al.* 2009). Severe storms are poised to become far more commonplace, mirroring a projected increase in harsher droughts in some of the driest portions of the United States. Most worrisome are the projections for future pest outbreaks. Forest pests and pathogens already affect an area 50 times greater than that affected by fire (Logan *et al.* 2003). Increasing temperatures are expected to expand the areas open to pest infiltration, virtually covering the entire continental US. This poses a significant problem since a portion of our historical emissions are housed within the forest canopies across the continent, and we

may need to rely upon them to alleviate future pollution as well. The combination of increased pest outbreaks and severe weather conditions would not only serve to drastically reduce our carbon storage capabilities but would also put a large portion of carbon back into the atmosphere.

With so much of our forest at risk, it is absolutely essential to understand what effects we are likely to see in the future. In the spring of 2008, a group working at the University of Michigan Biological Station (UMBS) began an experiment to examine those effects. Housed near the UMBS AmeriFlux site, the Forest Accelerated Succession Experiment (FASET) artificially accelerated succession from an aspen-dominated hardwood forest to a conifer-deciduous mixed forest by girdling the overaged early-successional species, *Populus spp.* and *Betula papyrifera*. The primary focuses of the experiment are to better understand the changes in carbon storage and cycling during and after succession. While originally crafted as an examination of forest succession, recent discussions have also coalesced on its importance in understanding the effects of pest outbreaks as well.

Thus far, a significant amount of time and effort has been spent analyzing those original goals of the experiment, and while much still remains to be understood, little to nothing is known about how such sudden changes in habitat will affect the biota within these forests. We selected the *Peromyscus leucopus*, or white-footed mouse, as our study subject due to its importance and abundance to the forests in this region (Baker 1983). As one of the most common mammals in these forests, *P. leucopus* functions as a primary food source for predators and a significant seed predator. Furthermore, the white-footed mouse is a disperser of mycorrhizal fungi, directly impacting the nutrient cycling of the ecosystem. As an ecosystem engineer, *P. leucopus* is an integral part of the proper functioning of these forests, and thus a natural starting point for an examination of the cascading impacts of experimentally-induced canopy dieback (Marshall *et al.* 2012). Furthermore, *P. leucopus* has an almost complete turnover of population from year to year, which should allow for any population shifts to start appearing now just four years after the beginning of the FASET manipulation.

In analyzing the effects of the FASET manipulations on *P. leucopus*, it is important to interpret change in context of metapopulation source-sink theory. Metapopulation theory is an important aspect of landscape and population ecology in that it defines various patches of habitat as either suitable, which can support a breeding population, and unsuitable, which are areas that are uninhabitable by a viable population (Wu 1994). Within these patches of area are subpopulations, which, when aggregated, form the overall metapopulation of the region. Source-sink theory takes this further by separating the patches into areas with optimal habitat – which would be exhibited by a population with higher birth rates than death rates – and suboptimal habitat – which is inhabited by a population with higher death rates than birth rates (Elmhagen and Angerbjorn 2001).

Within our study forest, there are already areas of unsuitable habitat, such as roads and other human-impacted areas. By girdling the dominants of the 33 hectare plot in the northern Lower Michigan forest, the researchers have also created two separate forest dynamics and, likely, two different mouse populations. What we seek to understand is whether or not this has resulted in a source or a sink dynamic within FASET for *P. leucopus*. To examine these questions, we conducted live trapping across multiple weeks in the summer of 2012. Since we anticipate the effects of the experiment at this time

point to be structural in nature, due to the increased availability of dead and dying trees, we measured both forest canopy density and downed woody debris (DWD) in parallel with the trapping. Through these measures, we aim to understand how the populations of *P. leucopus* have reacted to the forest changes in these past four years.

Furthermore, succession occurs on a much longer time scale than can be measured within a single summer, and hence, we anticipate continuing annual studies of the mice populations in these sites. This will allow us to fully understand what types of population dynamics to expect to see in the future.

## Methods

*Study Sites* – In order to examine the changes in population demographics of the *Peromyscus leucopus* following the girdling experiment, we set up trap-lines within two separate study areas:

- (1) FASET Plot: 45.56242° N, 84.69773° W; transitioning mixed conifer-deciduous forest with a relatively open canopy due to accelerated decline of overmature hardwoods; dominant tree species are white pine (*Pinus strobus*), sugar and red maple (*Acer saccharum* and *Acer rubrum*), big-toothed aspen (*Populus grandidentata*), and red oak (*Quercus rubra*)
- (2) Control Plot: transitioning mixed conifer-deciduous forest adjacent to the FASET plot; similar canopy species composition as in FASET with white pine, red oak, big-toothed aspen, and paper birch

We selected the adjacent forest as our comparison due to its proximity to the FASET plot (within 1 km) and similarity of pre-canopy manipulation forest composition.

*Trapping Methodology* – The positioning of the 6 trap-lines within FASET was dictated by the areas where relevant vegetation data has already been surveyed by other research groups. To minimize the effects of other research projects, all trap-lines in FASET began at a minimum of 30 m from the FASET Tower. The 3 control trap-lines were chosen in order to be the best comparison for what vegetation within FASET would be without the canopy manipulation (**Figure 1 → vegetation map**). To ensure their independence from any effects of the FASET plots, these control trap-lines were approximately 30 m from its closest point to the edge of the FASET plot. Each trap-line consisted of 30 small Sherman traps (6.5 cm x 5 cm x 16 cm) set at a minimum of 10 m intervals. One of the control trap-lines was kept to 20 traps due to a sudden shift to an open, mossy zone, which is irrelevant for comparisons with FASET. Traps were set and baited with oats at night and were checked the following morning. Each trapping session consisted of 2 consecutive nights of trapping. Each session consisted of 2 active FASET trap-lines and 1 control. To avoid adversely affecting local mice populations, each trap-line was not trapped for a minimum of 3 days after each trapping session. Trapping occurred for a total of 5 weeks, consisting of 1620 trapping hours. Age, sex, reproductive status, weight, parasite status, and trap location were logged for all trapped mice, and hind fur was clipped to distinguish between previously and newly caught mice. Age was determined by pelage condition, and mice were differentiated as adult, subadult, or juvenile. Reproductive status was broken into males with undescended testes (abdominal), males with descended testes (scrotal), females with nipples enlarged (NE), females with nipples not enlarged (NT), and pregnant females.

*Climate Data* – All climate data (air temperature, air humidity, wind speed and direction, and rainfall) were recorded from the AmeriFlux Tower which is within 2 km of all trapping stations. Only data between 9 pm and midnight were logged since that is the estimated hours of peak mice activity. A secondary climate variable that was measured was the phase percentage of the moon, which was used as a proxy for its overall luminosity and brightness.

*Habitat Data* – In order to ascertain exactly how the canopy manipulation was affecting the mice populations, a variety of habitat vegetation data was taken within the vicinity of the trap-lines. Percent canopy openness was measured using a spherical densiometer and taking the average of four separate readings at 90° angles from each other and multiplying that number by 1.04. This variable was also categorized into five classes: (1) <5%; (2) <10%; (3) <20%; (4) <40%; and (5) <55%. In order to get an estimate of the structural complexity available to the mice, we measured the distance to the nearest downed woody debris (DWD) at different size classes: (1) <0.5 cm; (2) 0.5-0.9 cm; (3) 1-1.9 cm; (4) 2-5 cm; and (5) 6-10 cm. We also focused further on the importance of DWD as habitat for *P. leucopus*, measuring the distance to the nearest fallen coarse woody debris (CWD), which was defined as anything greater than 5 cm in diameter. We then measured its diameter, and characterizing its bark and decay states. Bark condition was separated into five categories taken from Greenberg (2002): (1) 100% bark attached; (2) >70% bark attached; (3) >40% bark attached; (4) >10% bark attached; and (5) <10% bark attached. Decay state measures were adapted from the Forest Inventory Analysis (FIA) program of the USDA Forest Service (Woodall and Monleon 2008). Classification was based upon an evaluation of structural integrity, texture of rotted portions, and branch and twig condition.

*Data Analysis* – Population forcings or stresses often act on specific subsections of populations, which can cause noticeable differences in population demographics. When comparing sex, reproductive status, and age group, the  $\chi^2$ -test was used when appropriate and substituted with the Fisher's exact test when not. The two-sample t-test was used to compare weight distributions between the two populations. These comparisons were also broken down further in order to analyze differences in age classes and genders. All of the above distribution tests were conducted through Microsoft Excel 2010.

While the abovementioned tests analyzed the population demographics, it was also important to determine how these changes, if any, were occurring within the population. To look at these effects, we used *P. leucopus* catch success as a proxy for the populations on each trap night. It is important to note that when calculating this catch success, we considered the capture of any other species as a disturbance, therefore eliminating that trap from the general pool of available traps. Preliminary regression analyses were conducted to analyze the effects of the compiled weather variables on catch success. This was important in determining which factors had temporal and cyclical influences that we would need to identify when looking at trap-specific success rates. After calculating out individual trap success percentages, we used the vegetative data in a stepwise regression to understand what combination of variables had the most important influence on trap success. Such an extensive forest manipulation project can have several cascading effects, and these tests allowed us to pinpoint which vegetative variables were acting as the direct population forcing. To ensure that any trends seen were due to habitat differences and not population variation, we supplemented the regressions with direct comparisons between FASET and control areas of relevant vegetation variables using two-sample t-tests

and Mann-Whitney U tests. All statistical tests and graphical representations of population data was done through IBM SPSS Statistics (Version 19.0.0).

## Results

Over the course of five weeks of trapping (June 30 – August 1), which constituted approximately 1620 trapping nights, we caught 121 individual *P. leucopus* 261 times. Of those, 71 were caught within FASET and 50 were caught in the control trap-lines. We were able to get complete measurements for 61 of those in FASET and 49 in the control due to escapees. We also caught 80 *Tamias striatus*, although we are unable to determine the number of individuals since we did not mark them, as they were not our focal study species. Other species caught included two types of shrews, *Sorex cinereus* (5) and *Blarina brevicauda* (3).

*Population Demographics* – There was a noticeable difference in the overall distributions of *T. striatus* and *P. leucopus* catches between the control and FASET sites, including recaptures of the mice ( $\chi^2 = 15.15$ ,  $p < 0.0005$ ). There was a much higher frequency of *T. striatus* caught within FASET than in the adjacent forest (**Figure 2**). Within *P. leucopus* populations, however, there were three important categories in which the demographics differed between the FASET and control populations: reproductive status, weight, and botfly parasitism.

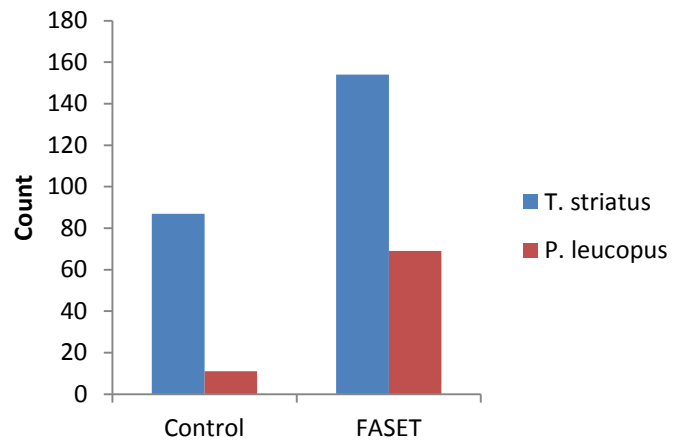


FIGURE 2. Comparison of capture totals of *T. striatus* and *P. leucopus* in control and FASET areas, University of Michigan Biological Station, Pellston, MI, USA.

While there were no differences in overall reproductive activity between the two sites, differences became apparent when the data were broken down by age group and gender. Within the adult age group, the control population had a greater number of reproductively active males, contrasting with a greater proportion of reproductively active females within FASET (Fisher's,  $p < 0.001$ ) (**Figure 3a**). In the subadult age group, however, the FASET mice population had a greater number of reproductively active males (Fisher's,  $p < 0.001$ ) (**Figure 3b**).

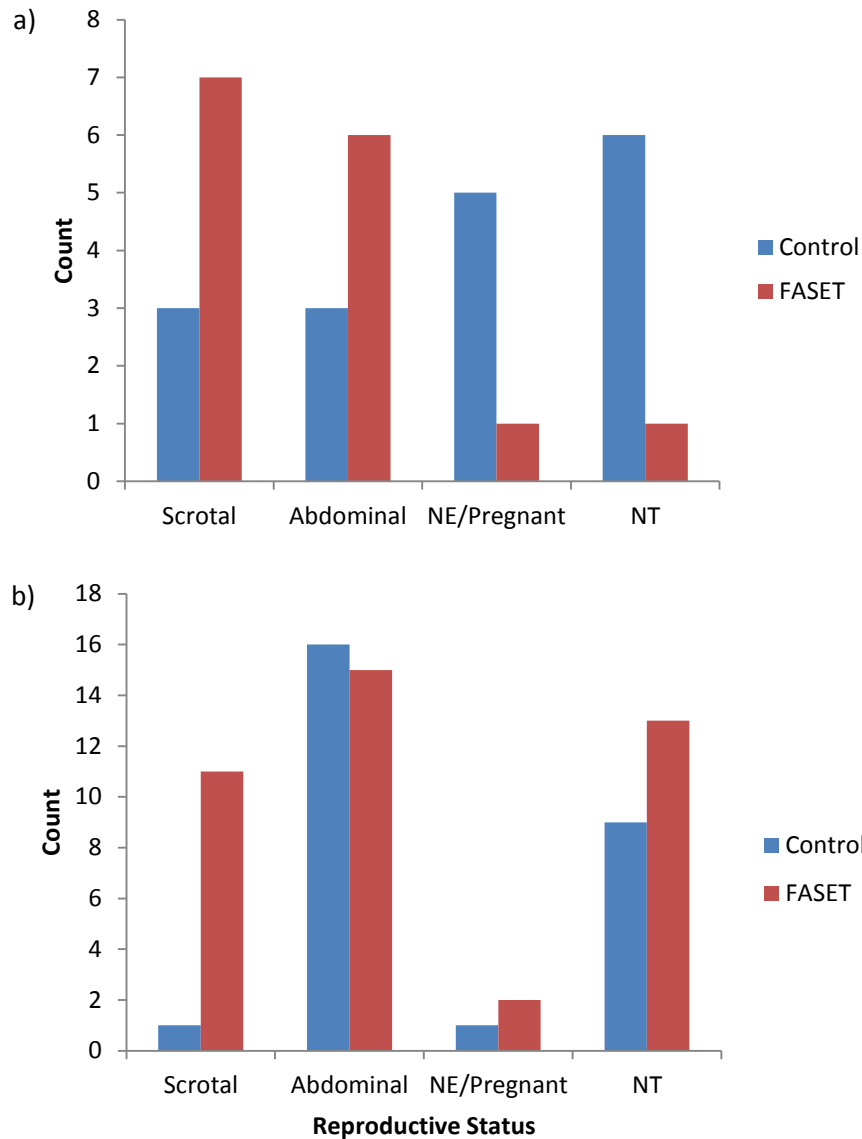


FIGURE 3. Comparison of reproductive status of a) adults and b) subadults counts between control and FASET areas, University of Michigan Biological Station, Pellston, MI, USA.

Similar to reproductive status, the weight distributions across the two overall populations were not different. However, the two populations exhibited weight differences between juveniles (Mann-Whitney U,  $p < 0.05$ ) and adult females (Mann-Whitney U,  $p < 0.05$ ), with the FASET population containing heavier juveniles (**Figure 4a**) and adult females (**Figure 4b**).

Finally, we observed an important difference in botfly parasitism. Mice caught in the control areas showed botfly parasitism at a much earlier time (July 20) when compared to those in FASET (July 31). Furthermore those that were parasitized in the control areas had much larger warbles. Within FASET, those botfly larvae that were detected seemed to have just appeared.

**Vegetative Influences** – Before proceeding, it is important to note that control trap-lines and FASET trap-lines had differing trap success rates (Kruskal-Wallis,  $p < 0.001$ ), with control trap-lines exhibiting far higher capture success rates (**Figure 5**). When comparing FASET and control areas using the measured vegetation variables, almost all exhibited significant differences (**Table 1**). In general, traps within FASET were closer in proximity to all DWD size classes and had larger pieces of CWD. While initially there was only a slight indication of differences in canopy openness, it became more evident when broken down into openness categories, showing that FASET had a more closed canopy than the control ( $\chi^2 = 21.04$ ,  $p < 0.0005$ ). Bark status was also significantly different between the two sites ( $\chi^2 = 10.07$ ,  $p < 0.05$ ).

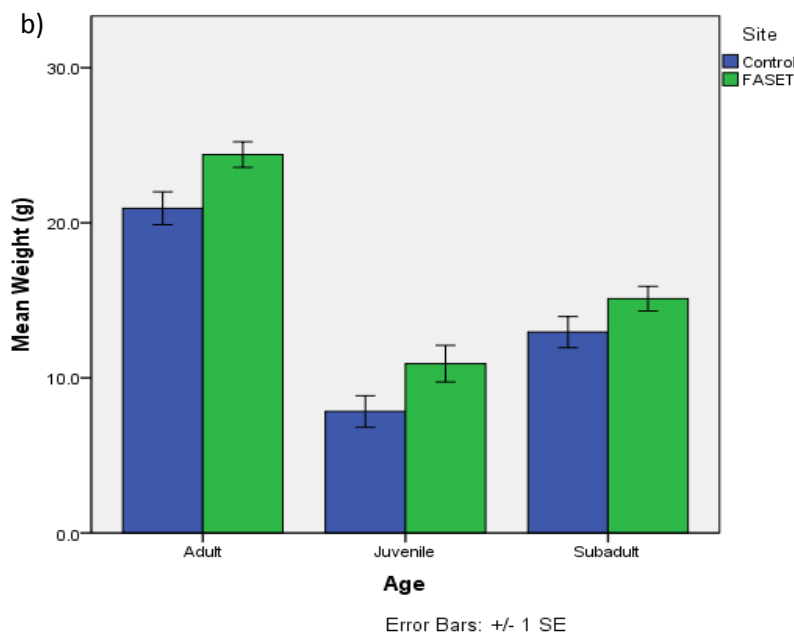
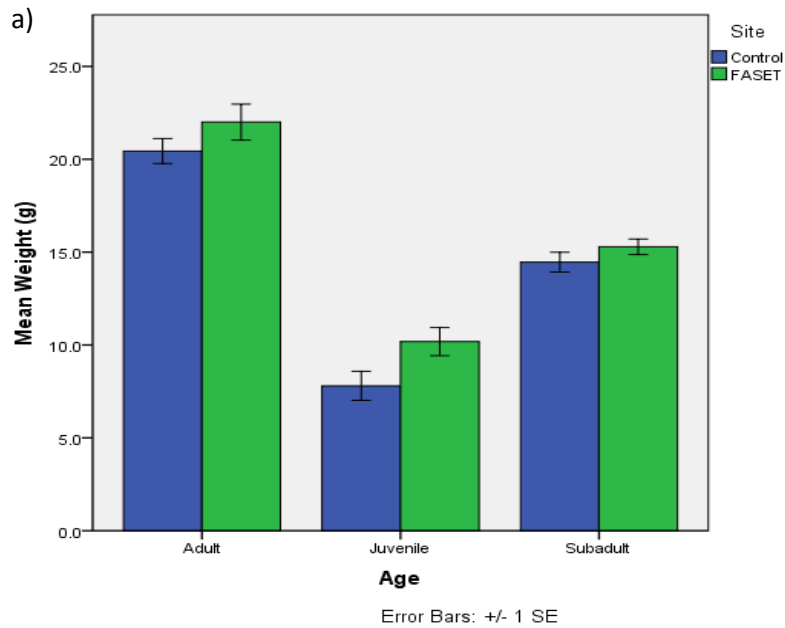


FIGURE 4. Comparison of weight (g) of a) all age groups and b) females between control and FASET areas, University of Michigan Biological Station, Pellston, MI, USA.

A stepwise regression was conducted using the following vegetative variables: percent canopy openness; distance to nearest piece of DWD of each size class; distance to nearest piece of CWD, its diameter, bark status, and decay status; and finally, average percent moon brightness across all nights trapped. While no combination of these variables was a significant predictor of catch success within the control sites, FASET had a series of important stepwise regressions. Of these, the most robust model included distance to the nearest DWD of diameter less than 0.5 cm (fine), percent canopy openness, and average moon brightness, which accounted for 4.9% of the variation in trap success at a p-value of less than 0.01. Specifically, trap success was negatively correlated with the distance to the fine DWDs and canopy openness, while positively correlated with moon brightness. Interesting to note, however, is that when trap success is regressed against those variables individually, only the distance to the fine DWD is significant ( $p < 0.05$ ). The other two variables showed some

indication of important trends, both with p-values of approximately 0.060.

While control areas as a whole were unable to be predicted by the measured vegetation indices, when isolated by trap-line, one very interesting pattern emerged. The BC trap-line, which begins on the western edge of FASET, was strongly correlated with the following variables: distance to DWD of diameter less than 0.5 cm and 2 cm, distance to nearest CWD, and distance to DWD of diameter less

than 1 cm, organized in order of their respective predictive power. The stepwise regression had a significance value of less than 0.005, predicting about 53.9% of trap success variation. Importantly, the distance to the three DWD size classes was positively correlated with trap success, while the distance to CWD was negatively correlated.

Stepwise regressions were also conducted against individual trap-lines within FASET as well, with only trap-lines A and C providing significant regressions. Trap-line A achieved a p-value of below 0.01, explaining 34.1% of its variation using distances to nearest DWD of sizes less than 0.5 cm (negative correlation), 2 cm (positive), and 5 cm (negative). Trap-line C had a p-value below 0.05, and explained 20.8% of its trap success variation using distance to nearest DWD of less than 0.5 cm (negative) and 1 cm (positive) and canopy openness (negative).

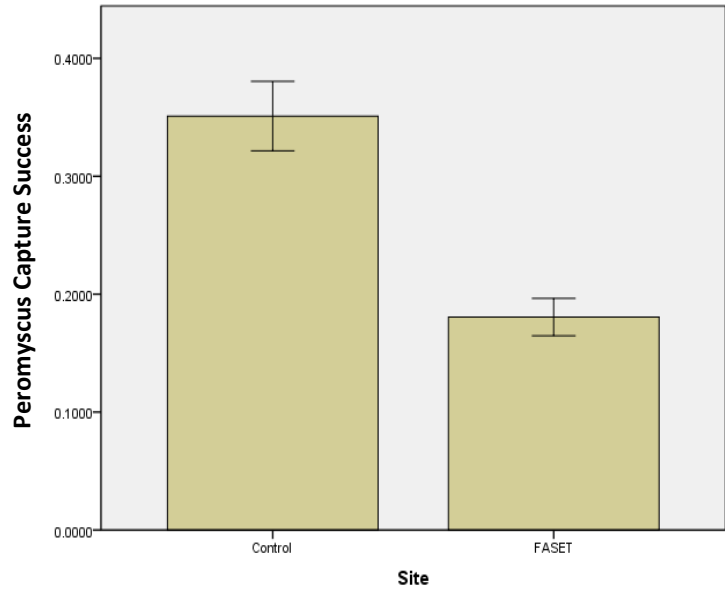


FIGURE 5. Comparison of average capture success percentages of *P. leucopus* in control and FASET areas, University of Michigan Biological Station, Pellston, MI, USA.

### Discussion

It has only been four years since the forest manipulation was completed in the spring of 2008, but due to the quick population turnover of *P. leucopus*, this means the populations have already gone through multiple generations since then, which is why we expected to see population shifts.

Variable	Test	Control	FASET	Significance
<0.5 cm DWD Distance	Kruskal-Wallis	17.932	9.547	0.001
<1 cm DWD Distance	Kruskal-Wallis	16.654	11.097	0.001
<2 cm DWD Distance	Kruskal-Wallis	35.671	24.862	0.001
<5 cm DWD Distance	Kruskal-Wallis	47.938	45.713	0.519
CWD Distance (cm)	Kruskal-Wallis	172.207	140.565	0.086
CWD Diameter (cm)	Kruskal-Wallis	11.835	15.044	0.012
Canopy Openness	Kruskal-Wallis	15.496	13.485	0.105
Moon Brightness	2-Sample T-Test	44.400	61.183	0.001

TABLE 1. Comparison of control and FASET areas based on measured vegetative variable means, University of Michigan Biological Station, Pellston, MI, USA.

**Reproductive Activity** – While we had originally hypothesized that shifts in age demographics would be indicative of differences in habitat quality, our results indicate that the most important demographic shifts are actually tied to reproductive activity. Interesting to note, however, are two seemingly contradictory storylines between the genders.



When looking solely at the female section of the population, FASET seems to contain a more optimal population dynamic (more reproductively active adult females that are heavier and heavier juveniles). That points to greater resource availability during reproduction for females, which potentially led to more physically fit (heavier) juvenile litters. This contrasts to when looking specifically at the male population, which as a greater number of reproductively active subadults within FASET and adults in the control. While the dominance structure within *P. leucopus* populations are not well understood, some preliminary studies indicate age as factoring heavily into that relationship (**London 1970**). In general, adult males maintain dominance over subadult males, which, in this context, points to a lower quality habitat within FASET.

This seemingly direct contradiction, however, can be better understood due to the differences in characterization of reproductive status for the two genders. Within males, being reproductively active simply means the testes are descended, meaning that copulation activity is a possibility. For females, however, reproductive activity is defined as being either pregnant or lactating, which indicates that the female has already undergone copulation activity. Therefore, the differing results may indicate differences in habitat selection depending on the reproductive stage of a mouse. Reproductively active males may seek areas with a greater density of female mice in oestrus, whereas pregnant or nesting females may seek out areas with a greater resource availability (**Metzgar 1971**). Such behavior would explain both the differences in weights as well as in reproductive status distributions.

*Botfly Parasitism* – While the parasitism results are not robust enough to draw any conclusions from, these preliminary observations may point to important differences in botfly persistence in response to changes in forest structure like that seen in FASET. Furthermore, botfly parasitism changes population dynamics in terms of competition and reproduction. Parasitized mice have been shown to be more physical fit and generally live longer than those without, with both of these factors scaling with number of botflies within a single mouse (**Cramer and Cameron 2007**). Furthermore, parasitized males are more aggressive and are, in fact, preferred by females for reproduction. These dynamics indicate the important influence of botfly parasitism on *P. leucopus* populations, and if botflies begin to show important responses to forest changes, that avenue of research will be critical towards understanding future populations of these mice. Future studies should focus more specifically on this question, perhaps bringing further understanding to not only the timeline of botfly parasitism in these areas, but also density, frequency within a single mouse, weights, among other variables.

*Vegetative Influences* – Both qualitative and quantitative measures of vegetation structure have been shown to be a strong determinant of population densities in general, as well as specifically with *P. leucopus* (**Morris 1988, McMurry et al. 1996, Anderson and Meikle 2006, Linzey et al. 2012**). Despite these historical results, however, the unmanipulated control forests of this study had no correlation between the selected vegetation structure indices and trap success. Part of this could be affected by the higher densities of mice within these areas, as indicated by the high overall trap success. Another possibility is the vegetation index itself; the variables that were measured were tailored specifically to the dynamics expected within FASET: dead and dying trees, more open canopies, and greater abundances of DWD. So while these variables were significant within FASET, they may be less relevant in intact forests. This is perhaps highlighted by the stark differences between control and FASET across

almost all those measured variables. The only variable without any indication of changes is the distance to the nearest DWD with a diameter of less than 5 cm.

The fact that the vegetation index was relevant within FASET and not across all control areas points to changing population dynamics of *P. leucopus*. As the forest begins its succession towards a more deciduous and conifer-dominated mixed forest, the forest dynamics that previously defined “ideal habitat” may be shifting. Some important facts to consider are not simply the greater availability of DWD due to the prevalence of dead trees, which are important corridors of movement for the mice, but also the growth of younger white pine, red maple, and other trees.

These shifting vegetation patterns help to explain the result that average moon brightness is, in fact, positively correlated with trapping success. While the actual forest canopy is open in many areas throughout FASET, this has already led to quickened growth of the undergrowth saplings. Due to the nature of measuring with a spherical densiometer, many trees as short as 2 m in height may have been included. Therefore a possible explanation for the positive influence of the moon is due to the increased availability of diffuse light at the forest floor, which, while helping the mice in foraging and navigation, does not cause them to be easily spotted by nocturnal predators.

The idea of shifting population forcings within FASET is further corroborated by the results of trap-line specific regressions of control areas. Since all three controls were spaced in widely differing areas, it was important to analyze them individually. The key result from this is the direction of correlation that the relevant variables had within this control site. While the positive relationship of DWDs of size classes 1 and 2 cm were also seen in some trap-lines within FASET, the positive relationship between trap success along the BC transect and the distance to nearest piece of fine DWD goes directly against what is seen within FASET.

*Inconsistencies in Trapping* – While the nocturnal and diurnal habits of *P. leucopus* and *T. striatus*, respectively, observations from this study may indicate the importance of their spatial relationships when it comes to studying those species specifically. Many traps were set during the late afternoon and early evening period, a time during which *T. striatus* are quite active. By setting off traps, knocking traps over, or even getting trapped themselves within the Sherman Traps, the chipmunks may have prevented the trapping of some *P. leucopus* whose ranges overlapped.

Another issue that may have affected the above interpretation of capture results is in the temporal nature of the moon cycle. The positive relationship of trapping success with moon brightness may be heavily influenced by the progression of *P. leucopus* populations over time. As the summer progresses, the populations undergo different reproductive and aging cycles, which may run parallel with the cycles of the moon. In future studies, it is recommended to increase the study length to encompass more full moon cycles to determine exactly which variables are most influential.

*Implications* – Despite seemingly contradictory results within the population demographics of *P. leucopus*, these are still preliminary indications that the induced forest succession is having an important ecological effect throughout the trophic levels. Furthermore, those contradictions may be explained by behavioral differences between genders and at different life stages. Unfortunately, it is impossible to

make a definitive statement due to the lack of depth in our understanding of *P. leucopus* biology. It is my recommendation that future studies seek to further our understanding of population dominance structures and reproductive cycles and behaviors so that future demographic studies can be more conclusive in their findings.

The most intriguing result from this study, however, is the indication that the population forcings of forest dynamics may be shifting. In reference to *P. leucopus*, the prevalence of dead aspen and birch has artificially increased the availability of DWD corridors, the vegetative cover from predators, and availability of diffuse moonlight. Outside of FASET, however, a different dynamic seems to be in place wherein the proximity of fine DWD is potentially a deterrent to capture. In order to truly understand what dynamics are at play within FASET and in undisturbed forest, a more focused study is necessary, perhaps analyzing a wider breadth of vegetation structure measures. Another important question is whether their other behaviors, many of which are critical in maintaining specific forest functionings, beyond foraging, are shifting as well.

Despite these preliminary results of changes both within *P. leucopus* population demographics and in their interactions with forests, it is still too early to distinguish whether a source or sink dynamic is at play within FASET. As climate change and its related effects continue to alter forest dynamics, oftentimes in very drastic ways similar to FASET, it is critical that we understand what population dynamics to expect. Otherwise, we may risk mismanaging these populations, resulting in detrimental population changes.

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