

What are the potential drivers behind the population dynamics of *Peromyscus maniculatus gracilis* and *Peromyscus leucopus* at the University of Notre Dame Environmental Research Center?

Sabrina Woo

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Advisor: Dr. Michael Cramer

Abstract

Studies have shown that with increasing climate changes, white footed deer mice *Peromyscus leucopus* has extended its range farther north, potentially displacing populations of woodland deer mice, *Peromyscus maniculatus gracilis*. Species differentiation has been understudied for these species of *Peromyscus*, so this investigation determined how climatic trends affect population densities for both *Peromyscus* species and if habitat selection or reproductive behavior can explain significant population differences between the two species. All data studied and collected was conducted at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan. A five-year dataset using expert trapping data, National Ecological Observation Network data, and field data was used for population and habitat selection analysis. The results found that precipitation has a significant effect on population density of *P. maniculatus*, reproduction behavior is affected by both species and time distribution, and habitat type has no relationship to capture success between species.

Introduction

Deer mice, *Peromyscus*, are widespread throughout North America but their ranges seem to be changing with global climate change. Studies have shown that with increasing frequency of shorter winters and earlier springs, *P. leucopus* has extended its range farther north (Meyers et al. 2009; Roy Dufresne et al., 2013), potentially displacing resident populations of *P. maniculatus* (Meyers et al. 2009). Current species coexistence research for *P. leucopus* and *P. maniculatus* has concluded that these species are equivalent in niche occupancy (Klein 1960), interspecific dominance behavior (Wolff et al. 1983), and diet (Wolff 1985); however, differences occur in foraging behavior (Cramer 2014) and more controversially, habitat selection (Wolff 1982; Barry et al. 1984; Bowker and Pearson 1985). Although both are considered habitat generalists (Drickamer 1987), *P. leucopus* may prefer habitats with more coarse woody debris, like tree fall gaps (Greenberg 2002; Persons and Eason 2019). If *P. leucopus* populations have changed their distribution over time, comparing habitat selection between the two species' may provide information concerning population displacement and competition. Additionally, any differences in reproduction behavior, as postulated by the northward expansion theory, should also support any differences in population sizes.

The northward expansion theory was tested at a specific location in the Upper Peninsula of Michigan, as populations of *P. maniculatus gracilis* are prevalent but *P. leucopus* are uncommon in this area. The present investigation will attempt to determine how climatic trends affect population densities for both UP *Peromyscus* species throughout the last five years and if habitat selection or reproductive behavior can explain significant population differences between the two species. The specific hypothesis being tested is that increased warmer weather leading into the fall will result in increases in *P. leucopus* population densities and decreases in *P.*

maniculatus gracilis, there will be reproduction differences between the species wherein *P. leucopus* will continue breeding further into the summer season, and that disturbed habitats will be more heavily populated by *P. leucopus*.

Methods

Study Area and Plot Selection

This study, along with all other long term data included, was conducted at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan (46°13'N 89°32'W).

To analyze current population estimates based on habitat type, two 100m x 25m transects were set in three types of disturbed sites: along the length of a powerline, within 100m of a building, and within tree fall gaps with canopy density < 75%. Five sites were chosen for each habitat type, with the exception of the building sites due to lack of available locations, and two replicates for each habitat were randomly selected to be sampled. All sites were at least 300km away from each other to ensure that there would be no migration between sites. Two additional sites were randomly selected from established trapping grids (Cramer 2019) within a closed maple forest habitat type for comparison to disturbed sites.

Long term population data analyses were based on two sources: expert trapping data from 2015 to 2018 (Cramer 2019) and National Ecological Observatory Network (NEON) trapping data from 2014 to 2018. Expert trapping data came from 8 different 60m x 60m grids established throughout the research center. NEON data included 90m x 90m grids deemed “pathogen sites”, listed as UNDE_012, UNDE_027, and UNDE_027.

Sampling Procedure

Sampling procedures throughout the varying data sources were similar. Sherman live traps were placed at 10-15m intervals throughout the grid/transect and set with bait before sunset and subsequently checked the next morning for three consecutive days. At the end of the three days, traps were set at a different site and the process repeated until all grids were completed in the constraint of the month. In the long term data, June, July, August, and September were sampled every year at all the sites for the full three days, barring unforeseen obstacles. Data collected for the habitat selection population estimates were conducted solely in July 2019. When mice were captured, species was indicated and field measurements like ear length, weight, sex, body length, and reproductive status (number of mammae, descended testes, pregnancy, or genitalia physiology) were included in the dataset. In addition, all mice that were captured were marked with uniquely numbered ear tags.

Statistical Analysis

The National Weather Service “Preliminary Monthly Climate Data” from Marquette, Michigan was used as a resource for climate data ranging from July 2014 to July 2019. All population estimates were calculated with the program MARK using individual capture histories under the assumption of a closed population for each grid, i.e. no migration or immigration on the study area and no births or deaths. Eight models (M0, Mt, Mb, Mtb, g*M0, g*Mt, g8Mb, g*Mtb) were selected to run each estimate and the best fit model ($\Delta AIC < 2$, parameter number < 4) was chosen as the population estimate for that site. Grids that captured less than five mice were also included with the population analysis using the minimum number known alive as a proxy for population size. Population estimates were then converted to density per kilometer to be used as a consistent comparison between data sources, given the varying plot areas of the

sample sites. Additionally, the reproductive score, a given number from 0-3 based on reproductive status (0- non reproductive, 1- testes descended or vagina open, 2 - pregnancy, 3- lactating female) was also calculated and included in the dataset.

Multiple statistical analyses were conducted to uncover potential population drivers behind *P. maniculatus gracilis* and *P. leucopus* based on climate, reproduction, and habitat selection. Using the combined means of the population densities over time, two time series from 2014-2018 were created displaying the two species' population trends by year and by each month sampled over the consecutive years. Preliminary tests like Shapiro-Wilks assessed the normality of the population density, the reproductive score, and the proportion of reproductive individuals. A log transformation was then conducted on the reproductive score and a logit transformation on the proportion of reproductive individuals to yield a normal distribution. Bartlett tests determined if there were equal variances between the species for population density, reproductive score, the proportion of reproductive individuals, and the average capture success (See Table 3).

After validating the data, Spearman correlation tests were used for climate analysis based on the concluded non-normal distribution and variance differences between the species population densities. Two Spearman tests were calculated using the combined population densities across time, regardless of species, against each climatic variable, average precipitation (inches) and average temperature (F°). Additional Spearman correlations were run separately by species, including data from all time periods, against the two climatic variables for species-specific correlations. The calculated difference between the species' densities was also used against the two climatic variables to determine if differences in species' population density over time were correlated with changes in climate.

For the reproduction analysis, a X^2 test was used to understand the relationship of year and species on reproductive individual counts. A 2-Way ANOVA was conducted to examine differences in the average reproductive score between *P. leucopus* and *P. maniculatus* based on month. Another 2-Way ANOVA was used to determine differences in the reproductive proportions and uncover any possible interactions using month and species as factors.

The Bartlett test of variance concluded that the capture success rate between species had unequal variances, thus the Mann Whitney U Test was performed to uncover any significant differences between *P. leucopus* and *P. maniculatus* capture success rates. A Kruskal- Wallis test was also used to assess for significant differences in capture success between habitat sites.

Results

The total population estimate size for *Peromyscus* was 2,714 mice over all the plots at UNDERC from 2014 to 2018. *P. leucopus* total population estimate was approximately 469 individuals and *P. maniculatus* was approximately 2,246 individuals over the entire time span (Table 1). It is assumed that no mice migrated between plots and that each plot was a closed population during each trapping period.

Time Series of Population Density. The population densities over each month vary, the greatest peak for population density occurring on August 2018 for *P. maniculatus* (6.08782 per km²) and July 2014 for *P. leucopus* (2.5232 mice per km²). Additionally, 2015 observed the lowest average population density for all years in both species, *P. leucopus* with 0.239 mice per km² and *P. maniculatus* with 2.063 mice per km² (Table 2). Each year is variable in the observed month for peak population densities between the two species (Figure 1).

Climate and Population Density. Spearman correlations indicate that there were multiple significant correlations between increased precipitation and increased population densities of *Peromyscus* (Table 4). *P. maniculatus* (p-value = 0.02) has a slightly positive correlation with precipitation (rho= 0.533), but *P. leucopus density* was found to have no correlation with summer precipitation or average temperature (p-value = 0.05427, 0.5). Similarly, no significant correlation was found for temperature for *P. maniculatus*. The calculated difference between the species' densities and precipitation yielded a significant result (p-value = 0.03229), determining that larger differences in species' population density are correlated with increased precipitation (rho= 0.496). These results combined indicate that greater gaps between densities are partly due to increasing *P. maniculatus* populations and varied *P. leucopus* populations during wetter weather.

Reproduction and Time Period. The X^2 test yielded results with significance, yearly observed counts of reproductive individuals is dependent on species ($X^2 = 16.4229$, p-value = .000929). The percentage of reproductive individuals based on the total count for each species observed throughout the years shows that there is an increase from 4.8% to 37.6% for *P. leucopus* from 2014 to 2018 (Table 5). 2018 is the only year where the proportion of *P. leucopus* is greater in comparison to *P. maniculatus*. Another X^2 test was run for species, month, and count of reproductive individuals, indicating a significant relationship between reproductive individuals of different *Peromyscus* species and the month (p-value is < 0.00001, see Table 5). A 2-Way ANOVA uncovered that the month (p = 0.00051) and the interaction of month and species affect the proportions of reproductive individuals (p = 0.001497). An additional 2-Way ANOVA examined differences in the average reproductive score between *P. leucopus* and *P. maniculatus* based on month, and found that there were significant relationships between the

month (p-value = 0.0336) and the interacting factors upon the reproductive score (p-value = 0.0288, see Figure 4).

Capture Success and Habitat Type. After the Bartlett assessment, it was shown that the capture success averages were varied between species. This is unsurprising as there were only two individuals of *P. leucopus* that were captured in total from all the sites. A Mann-Whitney U test was performed on the average capture success between the two species, regardless of habitat type and revealed a significant result (p-value = 0.01126), that there were differences between the two species' capture success averages and that capture success tend to be greater in *P. maniculatus* than *P. leucopus*. A Kruskal Wallis test was performed on capture success and habitat type (treefall gaps, powerlines, human building sites, and closed maple forests) and showed that habitat type had an insignificant relationship (df = 3, p-value = 0.32) to varying rates of capture success using combined *Peromyscus* data.

Discussion

Climate and Population Density. In this study, the varying results for the main hypothesis suggest many surprising conclusions for the population densities and presence of *Peromyscus*. The first aspect of the hypothesis was unsupported, in fact, the population densities of *Peromyscus* increase with the presence of more precipitation during the summer and have no relationship with increasing or decreasing summer temperature. Additionally, *P. maniculatus* consistently has a higher population density during wetter weather on average than *P. leucopus*. To understand this further, Morton et al. (1995) found decreased population densities of various species of *Peromyscus*, including *P. maniculatus*, during a period of drought and determined that water availability may be a factor in birth timing of mice. Additionally the effect of water

presence and reproduction is further suggested by Nelson (1993) who indicated that water restrictions can decrease reproductive activity within *P. maniculatus* males. However, this positive relationship is not concrete, precipitation during breeding season has been known to affect the relative mortality of female and male nestlings of *P. maniculatus borealis* (Havelka and Millar 1997). Precipitation is so variable that a study done by Rueppell et al (2002) on two populations of *P. maniculatus* yielded no significant correlations between precipitation and temperature to summer population growth. This null relationship has also been supported by Myers et al (1985) in a slightly different way, who found no correlation between rainfall in the summer and population of mice in the autumn. These potential effects of precipitation on population density and reproduction of *Peromyscus* is still debatable, but the relationship to time is definite.

Reproduction and Time Period. Populations of *Peromyscus*, like most small mammals, can fluctuate throughout the years, but follow a solid pattern of breeding and non-breeding season over the course of a year. Population spikes usually occur during the summer because the mice are breeding, but population differences between *P. leucopus* and *P. maniculatus* based on reproductive behavior has not been extensively studied. The northward expansion theory of *P. leucopus* suggests that earlier springs are allowing a likelier chance of *P. leucopus* surviving into the winter (Meyers et al 2005), but other studies suggest that the extended period of *P. leucopus* breeding season is a potential driver behind population increases (Rowland 2003). This study hypothesized that the occurrence of extended reproductive behavior would be a significant difference between species, supported by the results of the investigation. It was found that month and species were significantly related to multiple reproduction factors, the reproductive score and the proportion of reproductive individuals. Additionally, the interaction between month and

species upon those reproductive factors are important indicators that the reproductive differences between species are statistically significant throughout the summer months. Using Figure 4, it has been shown that there are more reproductive individuals and reproductive activity for *P. leucopus* during September in comparison to *P. maniculatus* across the four years and sites. Additionally, the majority of reproductive distribution for *P. maniculatus* is earlier in the summer, around June, and decreases by September. This finding provides significant evidence for population analysis if studied further, considering the long term implications of population replacement or competition from advantageous breeding periods.

Capture Success and Habitat Type. The last aspect of this study's hypothesis was unsupported by the data collected in the field. Species capture successes were considered statistically different, due to the lack of *P. leucopus* individuals caught at the sites and the common occurrence of *P. maniculatus* at almost all of the sites (Figure 6). The population analysis of this study saw the greatest number of *P. leucopus* just in the last year, which makes it more surprising that only two *P. leucopus* individuals were caught. These results of this study may be due to a variety of factors. Although there were no significant results for *P. leucopus* density and precipitation, climatic factors affecting the winter survival of mice may be more important than the weather within the summer (Heisler 2014). Furthermore, a polar vortex hit during the last winter and it has been shown that *P. maniculatus* are better winter specialists than *P. leucopus* (Pierce and Vogt 1993). Mice that stay in uncovered habitats are also vulnerable to predation and may become disoriented if they stray too far from the forest edge (Zollner and Lima 1997). This may explain the lack of difference in capture success between the varying habitat types (Figure 5).

The data used in this study was extensive and came from various sources, allowing variability in data comprehensiveness and accuracy from each source to potentially accumulate in the dataset. For example, the NEON dataset was occasionally inconsistent in taking field measurements given the large volume of mice the organization processes on each grid. Some mice could be marked a different species, sex, or have ear lengths measuring from 14mm-19mm in the course of the three trapping days or between the months. However, any individual data point that was contested without further evidence available to identify it to the correct species was discarded from the dataset. Samples in all datasets that were not identified to species, perhaps due to escape during measurements, were also excluded from the data. Carnivore attacks, like bears and raccoons, were also obstacles that could have significant effects on the population estimates, especially if trapping concluded earlier than expected. However, grids that were only trapped one day were excluded from the dataset and non-consecutive trapping days were also discarded. Another limitation to this study was that only two replicates for each site were used for the habitat selection analysis, making the capture data less significant with the small sample size and lack of replication. A comparable study should use more replicates and habitats, perhaps ensuring consistent vegetation throughout the habitat types. Additionally, the last day of trapping for the habitat transects had a variable ratio of bait, further conflicting the capture success data.

Future studies using the population estimates of all breeding, post-breeding, and non-breeding seasons to focus on climatic factors affecting population, especially during the winter, would be beneficial to further explain population density differences. Factors affecting winter survival and thus the population of *Peromyscus*, could be explained by a long term observational study of nest boxes during the winter and possibly conclude species-specific behavior patterns.

Parsing out the genetics of specific populations of mice across the Upper Peninsula may also lead to significant conclusions for the historical and eventual distribution of *P. leucopus* and *P. maniculatus*. Additionally, compiling the remaining NEON sites across the Upper Peninsula, or even across North America, would be a significant resource for the current geographical distribution and population of *Peromyscus* and other small mammals. Studies of vegetation for preferred habitat sites and ecosystem overlaps in home ranges would also be a useful study to investigate habitat selection of deer mice. Overall, species differentiation between *P. leucopus* and *P. maniculatus* are important sources for population studies and significant indicators of changing behaviors under climate change.

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Table 1: The sum of population estimates from MARK, including all grid data collected from each year. The year 2014 included only the NEON dataset, due to data availability.

Grids	Plev	Pman	Sum Pq
2014	92.55289	285.3828	377.9357
UNDE_012	13	71.32463	84.32463
UNDE_027	68.00712	178.3596	246.3667
UNDE_032	11.54577	35.69864	47.24441
2015	41	288.6239	329.6239
BONO	0	22	22
CBRY	2	23	25
CRMN	0	27	27
DBOG	2	28	30
HKQK	7	34.42966	41.42966
NRTH	4	24	28
PLUM	0	15	15
STOR	5	50.19422	55.19422
UNDE_012	4	20	24
UNDE_027	17	35	52
UNDE_032	0	10	10
2016	56	449.7697	505.7697
BONO	5	45.3995	50.3995
CBRY	2	52.988	54.988
CRMN	1	48.06494	49.06494
DBOG	0	40	40
HKQK	6	39.00072	45.00072
NRTH	4	32.71299	36.71299
PLUM	4	49.73847	53.73847
STOR	12	50.79819	62.79819
UNDE_012	13	30	43
UNDE_027	6	40.29098	46.29098
UNDE_032	3	20.7759	23.7759
2017	121.7072	633.2966	755.0038
BONO	11	70.38674	81.38674
CBRY	11	52.00001	63.00001
CRMN	4	73.12214	77.12214
DBOG	4	34.05751	38.05751
HKQK	6	45	51
NRTH	14.05514	22	36.05514
PLUM	4	61.67145	65.67145
STOR	20	68.21996	88.21996
UNDE_012	2	36.87084	38.87084
UNDE_027	42.65207	156.9679	199.62
UNDE_032	3	13	16
2018	157.491	588.8009	746.2919
BONO	11	48.61873	59.61873
CBRY	12.10137	53.58309	65.68446
CRMN	17.23146	48.3728	65.60426
DBOG	9.297443	25.70087	34.99831
HKQK	20.64079	51.89765	72.53845
NRTH	4	49.80313	53.80313
PLUM	5	31.69101	36.69101
STOR	26.66796	66.26484	92.93281
UNDE_012	8	49	57
UNDE_027	39.55201	132.2238	171.7758
UNDE_032	4	31.64498	35.64498
Grand Total	468.7511	2245.874	2714.625

Table 2: The average population density per kilometer for each year, seperated into months.

Population densities include all sites trapped in that month and year.

Years	Months	Pleu	Pman	AVG Pop Density
2014		1.632326	5.033207	3.332766561
	July	2.523156	4.913216	3.718186049
	August	1.505561	5.191093	3.348326914
	September	0.931644	4.916369	2.924006543
2015		0.239651	2.063013	1.151332108
	June	0.064815	1.063332	0.564073559
	July	0.288066	0.740741	0.514403292
	August	0.325477	2.738551	1.532014212
	September	0.305556	2.716282	1.510918986
2016		0.357662	3.26125	1.809455651
	June	0.027778	1.280709	0.654243315
	July	0.164609	0.699588	0.432098765
	August	0.43771	3.900097	2.168903899
	September	0.657407	5.307557	2.982481981
2017		0.755824	4.114176	2.43499999
	June	0.328235	2.847841	1.588038334
	July	0.370291	2.260557	1.315424023
	August	1.048829	4.744395	2.896611978
	September	1.019527	5.369988	3.194757414
2018		1.084605	3.960778	2.522691503
	June	0.221661	1.079443	0.650551782
	July	0.445452	1.618685	1.03206858
	August	1.316321	6.08782	3.702070588
	September	2.094901	5.89973	3.997315373
Grand Total		0.657208	3.433281	2.045244538

Table 3: Bartlett tests assessed different continuous variables for variance. Capture success and population density were observed to have variance between species ($p < 0.05$). Any variable known to have variance were subjected to non-parametric tests.

~Species	K-squared	df	p-value
PopDensity	15.481,	1	8.34E-05
Score	1.0706,	1	0.3008
Log Score	0.08874,	1	0.7658
Log Repro%	1.0859,	1	0.2974
Capture%	6.3726,	1	0.01159

Table 4: Spearman correlation tests assessed climatic variables relationships to species' population density. The label "Dif Density" is the calculated difference between species' average population densities.

Subject	Variable	p-value	rho
All Species	Precip	0.0458	0.325976
	Temp	0.2489	-0.19172
<i>P. man</i>	Precip	0.02029	0.5333
	Temp	0.1005	-0.38823
<i>P. leu</i>	Precip	0.05427	0.450877
	Temp	0.5063	-0.16249
Dif Density	Precip	0.03229	0.496491
	Temp	0.05604	-0.44532

Table 5: The chi-square statistic is 16.4229. p-value = .000929, df = 4

Species	2015	2016	2017	2018	Row Totals
Pleu	4.80%	22.40%	35.20%	37.60%	100.00%
Pman	12.62%	29.21%	36.39%	21.78%	100.00%
Totals	17.42%	51.61%	71.59%	59.38%	100.00%

Table 6: The chi-square statistic is 37.2856. The p-value is < 0.00001. The result is significant at $p < .05$.

Species	June	Aug	Sep	Row Total
Pleu	14.40%	55.20%	30.40%	100%
Pman	42.57%	42.82%	14.60%	100%
Totals	56.97%	98.02%	45.00%	100%

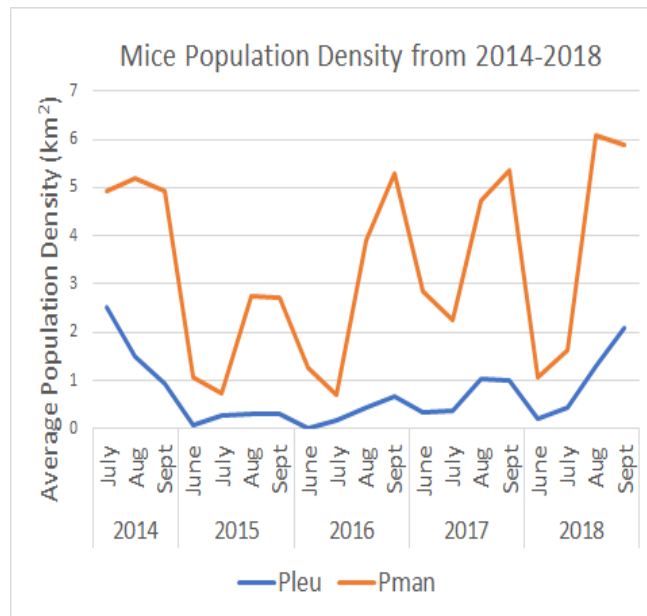
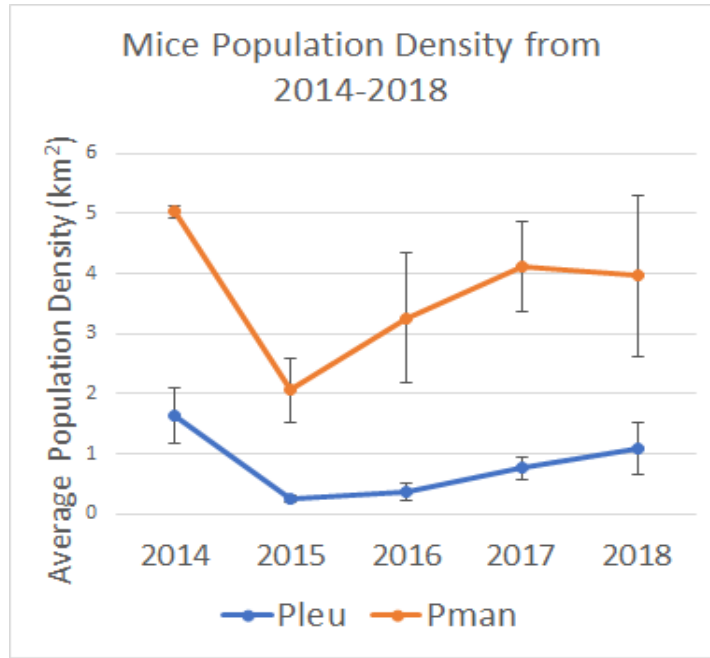


Figure 1: Population densities averaged by year, dataset only includes months from June-September. The year 2014 includes only 3 NEON plots, all other years include 11 plots. Population densities for *P. maniculatus* varied greatly during the months of 2018, increasing the probable range of actual population densities for that year.

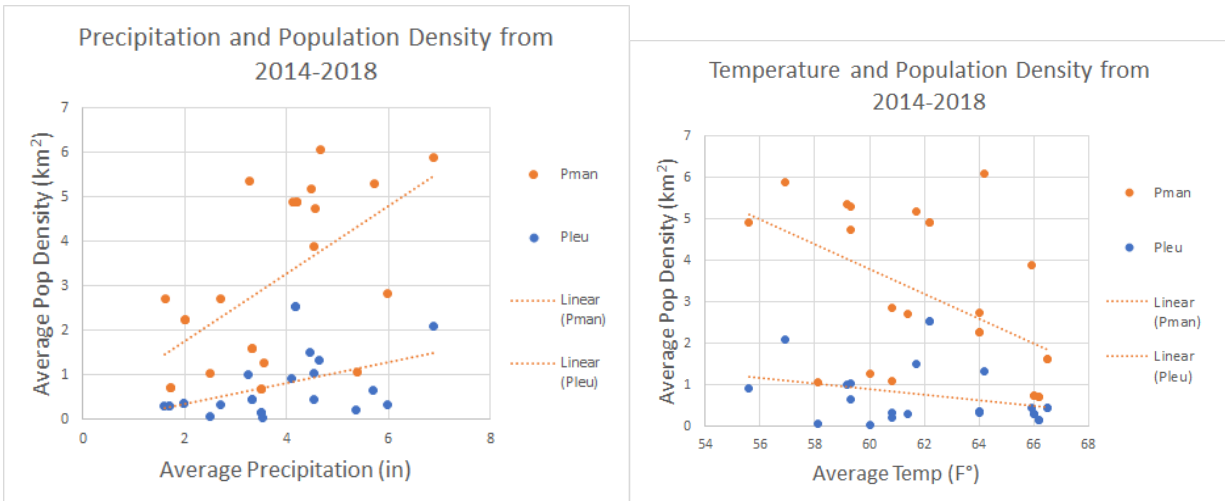


Figure 2: The figures above are regressions of average population densities and climate. Species specific series are displayed. Spearman correlations indicate that there is a significant correlation between increased precipitation and increased population densities of *P. maniculatus* (p-value = 0.02) and *P. leucopus* (p-value = 0.05427). No significant correlation for temperature for either species.

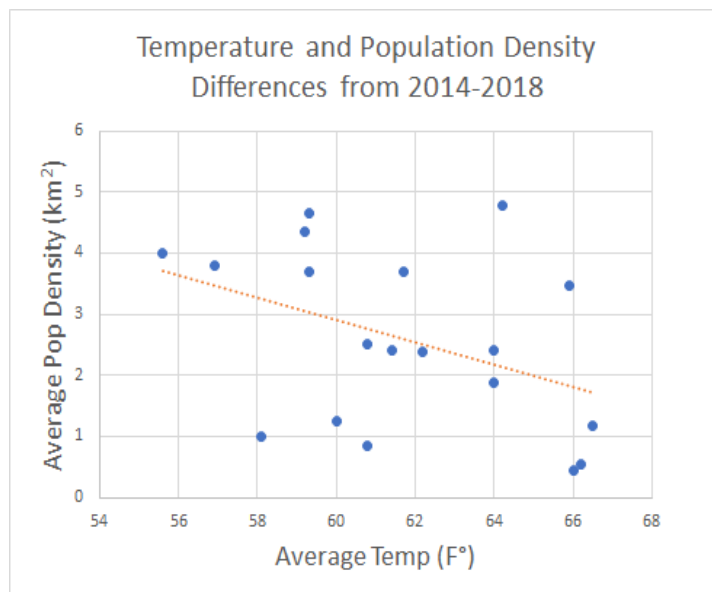
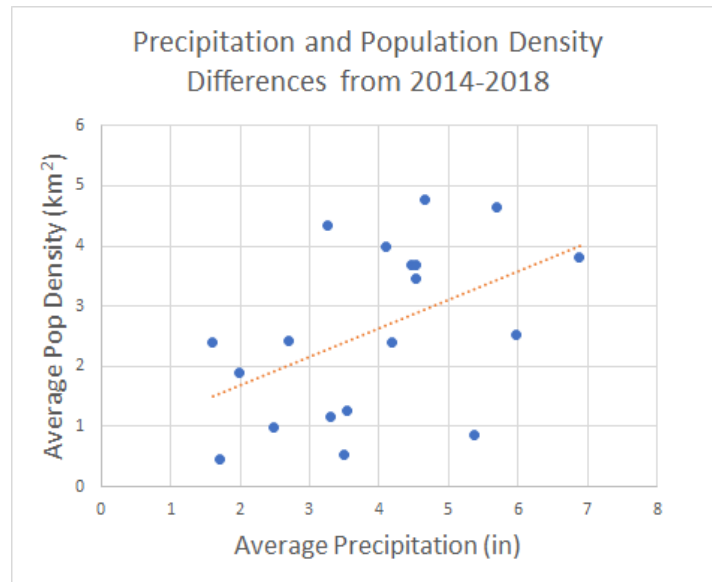


Figure 3: The difference was calculated by subtracting the population density averages of *P. leucopus* from the population density averages of *P. maniculatus*. The calculated difference between the species' densities and precipitation yielded a significant result (p -value = 0.03229), determining that larger differences in species' population density are correlated with increased precipitation (ρ = 0.496). Temperature yielded no significant results (p -value = 0.05604)

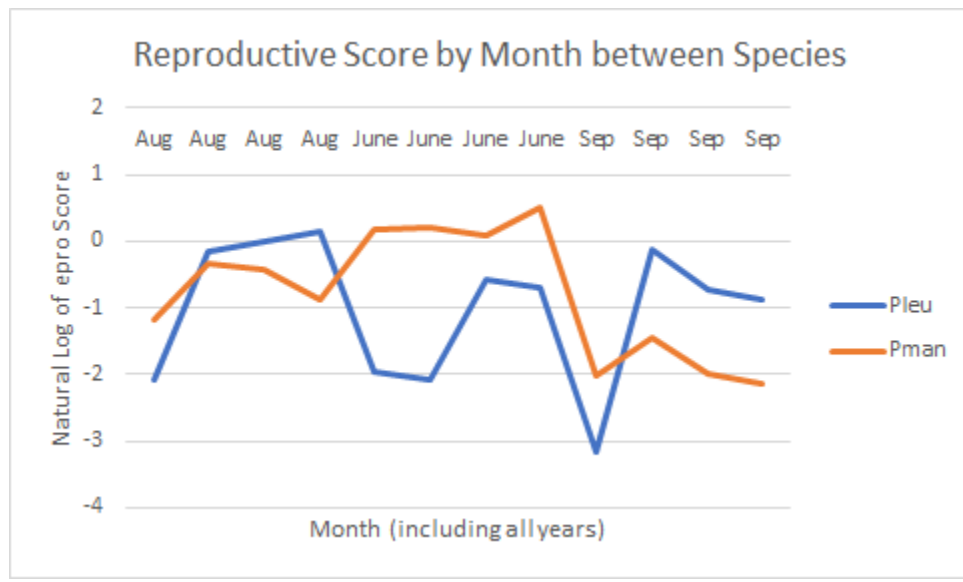
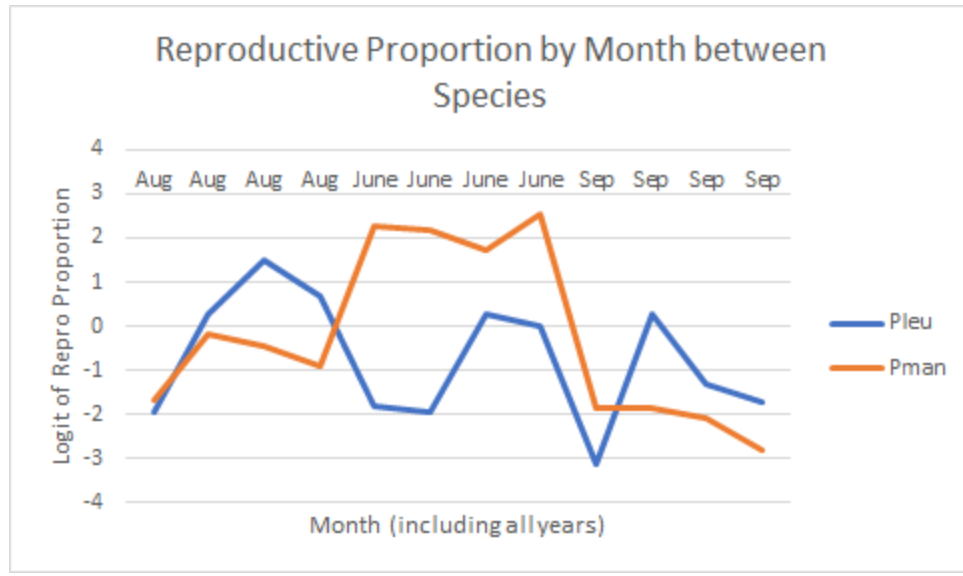


Figure 4: Above are graphic representations of 2- Way ANOVAs that were found to be significant for both reproductive variables. Both month and the interaction between month and species were considered significant for the reproductive score ($p = 0.0336, 0.0288$). The same factors were considered significant for proportion of reproductive individuals ($p = 0.000511, 0.001497$)

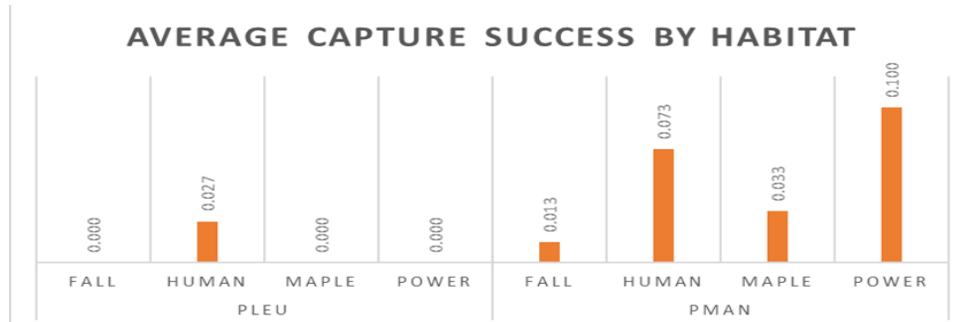


Figure 5: Kruskal-Wallis was used to analyze the capture success and habitat type. No significant result was found. (df = 3, p-value = 0.3196). Closed maple forests were used as a comparison to the three other disturbed sites.

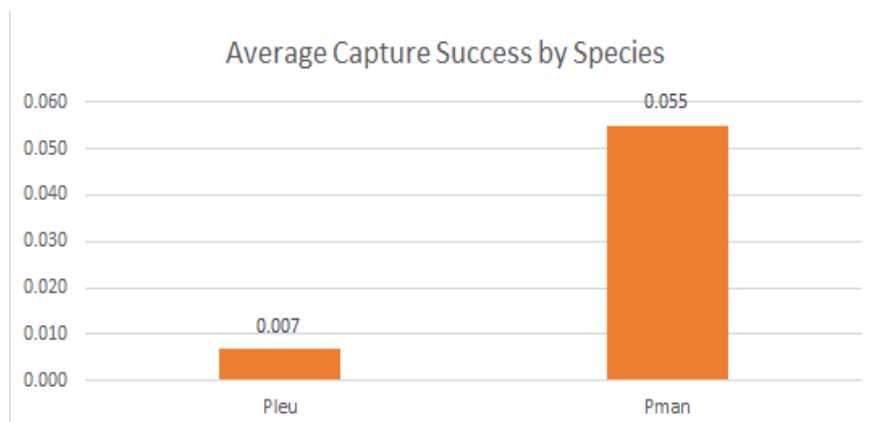


Figure 6: Based on a Mann Whitney U test, the differences between the capture success and the species is significant, with observations skewing towards greater captures for *P. maniculatus* (p-value = 0.01126)