

**The primacy effects of seasonal shifts on the foraging behavior of
wild-caught woodland deer mice (*Peromyscus maniculatus gracilis*)**

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Dominic J. Acri¹

Advisor: Michael J. Cramer¹

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¹ University of Notre Dame Environmental Research Center, Department of Biology,
University of Notre Dame, IN 46556

Abstract

This study explores the immediate shifts in foraging behavior of woodland deer mice (*Peromyscus maniculatus gracilis*) caused by sudden onset of fall weather. The immediate effects of a shift in seasonality include a significantly delayed onset of nocturnal activity, but do not include a shift in offset of nocturnal activity. A study on deer mice has shown the species-specific feeding preferences (Cramer 2014); our study found that such preferences are altered after experimental seasonal shifts. Under the stress of a shift in seasonality, *P. m. gracilis* show an increased preference for *Acer saccharum* seeds. Further analysis of foraging behavior, through an index which calculates the probability that uneaten seeds were handled, suggests that *P. m. gracilis* are more likely to handle *A. saccharum* seeds under fall conditions. The shift in foraging behavior caused by the primacy effects of seasonal shifts supports the hypothesis that these foraging behaviors have an underlying seasonal rhythm.

Introduction

Rhythmic changes in foraging are evident through observable behavior; when adapted behaviors vary by annual environmental cycles, they are known as seasonal rhythms. Foraging behaviors, such as preferences for certain food items, could be explained by the need for more energy and increased maximal metabolic rate during colder seasons (Sears et al., 2009). These behaviors are the result of natural selection over countless generations, but climate change has introduced unpredictable fluctuations in seasonality such as unseasonably cold fall and winter months (Jalili et al., 2010; Sears et al., 2009). Animals that are maladapted to the climate in their area could be more susceptible to predation, unprepared to survive food shortages, and less prepared when the climate shifts back to the original season, which would lower survivorship.

The woodland deer mouse (*Peromyscus maniculatus gracilis*) is an omnivorous generalist that displays selectivity for *Acer rubrum* over *Acer saccharum* seeds (Cramer 2014); *A. rubrum* have shells approximately one-fifth in size when compared to *A. saccharum* (Moles et al., 2003). Preference for a food source is a behavior that could

have adapted out of competition, altered resource availability, or a confounding evolutionary advantage. Although the larger seeds would be preferable for seed predators, the increased handling time associated with thicker shells may affect the risk-nutrient payout.

Changes to photoperiod and temperature—as they relate to seasonality—have the potential to alter an animal's normal foraging behaviors and preference for seed type; it is yet unknown what role seasonal photoperiod and temperature shifts play in foraging behavior and what effects are present immediately after these shifts in the environment. Studying these effects could inform at least one of the immediate dangers of climate change.

P. maniculatus and trees of the genus *Acer* (specifically *A. saccharum*) both exhibit rhythmic behaviors that could explain the seasonal differences in foraging behaviors (Reid and Brooks 1993; Lambers and Clark 2005). By holding the availability of *Acer* seeds constant, seasonally-shifted behavior could be studied independent of food availability. The effect of light-induced shifts on the nocturnal activity of *Peromyscus* remains conserved in wild-caught and first generation captive-bred mice (Layne 1971); therefore wild-caught mice should exhibit the same primacy effects of these shifts during short-term experiments as their captive-bred counterparts.

Climate change, as it relates to unpredictability in climate, has implications for population dynamics, speciation, and disease transmission in *Peromyscus*. Differences in seasonally dependent factors can affect populations of small mammals (Klimstra et al., 2015); if these population factors are related to seasonal rhythms, they may also pose a possible explanation for foraging differences across seasons. Niche overlap and

competition vary seasonally in sympatric species of the genus *Peromyscus* (Llewellyn and Jenkins 1987). Transmission of viruses in *P. m. gracilis* is dependent on seasonal shifts in behavior, which could be due to the confounding effect of population density (Bagamian et al., 2010; Luis et al., 2010). These changes in behavior could be implicated similarly for foraging behaviors—the focus of this study. A link between seasonal shifts and foraging behavior may uncover an integral part of hantavirus-host dynamics or Lyme Disease host dynamics that lead to an increase in the *P. maniculatus* populations (Paull and Johnson, 2014). Because small mammals can have a large impact on ecosystems, understanding how seasonal shifts affect their foraging behavior will provide insight for wildlife management and conservation on a larger scale.

Shifts in behavior are important to understand with the increasing effects of climate change. Several studies have already begun to investigate how climate change affects wildlife (Skerritt 2002). Artificially warmed experimental food bins for *P. maniculatus* and *P. leucopus* during the winter produce the opposite effect that this study proposes (St. Juliana and Mitchell 2016). Although this study measures a different factor under the opposite conditions, it supports the existence of a persistent, yet-adjustable seasonal rhythmicity. A similar model for climate change predicts the effect of seasonal confusion on female turtles' ability to shift nesting dates (Telemenco et al. 2013). The literature on this topic is sparse; researchers have mentioned that more work needs to be done to “[understand] the various factors that govern the timing of daily activities” (Shuai et al., 2014).

This study explores the immediate shifts in foraging behavior, measured through seed selectivity and foraging preference, of woodland deer mice (*Peromyscus*

maniculatus gracilis) caused by sudden onset of fall climate. We hypothesize that sudden onset of fall temperature and shortened day length will (1) shift the animals' activity to adjust for the longer nocturnal period, (2) result in a neutral selectivity for seeds of the genus *Acer*, and (3) increase in consumption of high-nutrition, high-handling time seeds (*Acer saccharum*).

Methodology

Trapping Protocol

Trapping was conducted at the University of Notre Dame Environmental Research Center (UNDERC), located on the border of Wisconsin and the Upper Peninsula of Michigan (46°13 N, 89°32 W). Trapping transects were selected in forest stands dominated by trees of the genus *Acer*, which had been used in previous studies (Figure 1; Cramer 2014). *P. m. gracilis* were live-trapped using Sherman traps (7.62 cm × 8.89 cm × 22.86 cm; H.B. Sherman Traps, Inc., Tallahassee, Florida, USA) baited with approximately 5 g of black oil sunflower seeds and bird seed. All captured animals were marked with ear tags. Ear biopsies were taken for species confirmation, if necessary; previous studies have confirmed that ear length field identification is sufficient for identifying *P. m. gracilis* in the field (Ridenhour and Cramer 2014). Lactating or pregnant females were released upon capture, because their foraging demands are physiologically complicated.

Seasonality Shift

Mice were housed in individual cages (19 cm x 29 cm x 12.5 cm) with corn cob bedding, polyfill nesting material, food (rat chow), and water *ad libitum*. The mice were subjected to one of two conditions in a climate-controlled incubator: summer (control)

and fall. The summer condition was set to a temperature and light-dark (LD) cycle consistent with the June averages in the area: 16:8 LD cycle and an average temperature of 25 °C (National Oceanic and Atmospheric Administration, Rhinelander, WI). The fall condition was set according to the temperature and LD cycle consistent with September averages in the area: 13:11 LD cycle and an average temperature of 15 °C (National Oceanic and Atmospheric Administration, Rhinelander, WI). Sunrise and sunset were simulated with gradual 30-minute light-on and light-off periods.

The animals were observed for 3 days and their activity was scored according to visible locomotion (feeding, nesting, escape behavior, etc.) outside of the housing unit via video analysis (Night Owl Security, 2015). Every 10th minute, each mouse received a score of 1-60 indicating the seconds active during that minute. All time points were then reported in local clock time (Central Standard Time; UTC-5:00).

Quantification of Seed Preference and Foraging Behavior

Five hours prior to testing, the food was removed and recording for locomotion activity ceased. Five grams each of dried *A. saccharum* and *A. rubrum* seeds were weighed to the nearest 0.01 g and placed in petri dish in the mouse's cage. Seeds were obtained from professional seed companies (Sheffield's Seed Co., Inc., Locke, NY, USA). Seed preference trials began one hour prior to relative dusk and continued until approximately one hour after relative dawn. After the trial, uneaten seeds were categorized as either non-foraged (in dish + surrounding 4.1 cm around dish to control for seeds displaced by feeding) or foraged (> 4.1 cm from location of the dish) and weighed. Mice were released back to the trapping grid on which they were caught.

Statistical Analysis

A median score of activity was calculated for each individual (on minute basis) and averaged across animals of the similar condition (summer or fall). These data were plotted in 1-minute bins for visualization purposes with score as the dependent variable and time as the independent variable. Onset of nocturnal behavior was defined as three consecutive time points of at least an activity score of 20; offset of nocturnal behavior was defined as three consecutive time points of an activity score less than 20. Both onset and offset of nocturnal behavior were analyzed using a Student's t-test with score as the dependent variable and time as the independent variable; nonparametric analysis was run when data failed normality tests with and without transformations. Differences between the two trial conditions, summer and fall, were used to assess the efficacy of the seasonal shift.

Selectivity for the seed type used forage ratios: p_c/p_a , where p_c is the proportion of consumed seeds that were type i and p_a is the proportion of all available seeds that were type i (Page et al. 2001). The difference in selectivity (*A. saccharum* minus *A. rubrum*) was analyzed to compare the relative preferences; the preference index, therefore, ranges between -2 and 2. Mice with a preference index of -2 showed a complete selectivity for *A. rubrum*, while mice with a preference index of 2 showed a complete selectivity for *A. saccharum* (Cramer 2014). Data were analyzed with a Student's t-test with preference index as the dependent variable and seasonality as the independent variable; nonparametric analysis was run when data failed normality tests with and without transformations.

A similar ratio was used to compute foraging scores, where p_c is the proportion of foraged seeds that were type i and p_a is the proportion of all available seeds that

were type *i* that were not consumed. The difference in foraging score of the same seed type (seeds found outside the dish minus seeds found in the dish) quantified the likelihood that uneaten seeds were handled. The difference in handling (*A. rubrum* minus *A. saccharum*) was analyzed to compare foraging behaviors with respect to seed type; the foraging index ranges between -2 and 2. Mice with a foraging index of -2 moved all uneaten *A. rubrum* seeds; while mice with a foraging index of 2 moved all uneaten *A. saccharum* seeds. The foraging index controls for amount eaten by only taking into account uneaten seeds. Data was analyzed with a Student's t-test with foraging index as the dependent variable and seasonality as the independent variable.

All statistical analyses were conducted with R release 3.1.2 (R Development Core Team 2014) and R Studio version 0.98.1091 (R Studio, Inc. 2014). All animal use conformed to the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and the Animal Behavior Society (Ethical and Animal Care Committee of the Animal Behavior Society 2012) and was approved by the Institutional Animal Care and Use Committee at the University of Notre Dame (protocol 14-04-1722). All statistics are reported as means \pm SE unless otherwise noted.

Results

A total of 30 (25 male and 5 female) mice were caught on trapping sites (Figure 1) and kept for holding and trial during June and July 2016. Although the weights of mice in both trials was not normal ($W = 0.8518$, $p < 0.05$), Mann-Whitney U test showed no significant difference between seasons ($U = 71.5$, $p > 0.05$). Two mice did not complete trials either due to death or abnormal behavior. Other specimens caught include *P. leucopus*, *Sorex cinereus*, *Zapus hudsonius*, *Napaeozapus insignis*, *Tamias*

striatus, and *Bufo americanus*; all of these animals were released when traps were checked.

Onset time of mice in the summer treatment passed the Shapiro-Wilk normality test ($W = 0.8907$, $p > 0.05$), but onset time of mice in the fall treatment failed ($W = 0.8186$, $p > 0.05$). Nonparametric analysis via Mann Whitney U test reported a significant difference between the onset times in the two treatments ($U = 33.5$, $p = 0.003$; Figure 2a). Offset time of mice in the summer and fall treatments passed the Shapiro-Wilk normality test (Summer, $W = 0.9201$, $p > 0.05$; Fall $W = 0.9217$, $p > 0.05$). A Student's t-test revealed no significant difference between offset times in the two treatments ($t = -0.934$, $df = 26$, $p > 0.05$; Figure 2b). The 24 hour activity of summer and fall treatments reveal very little activity during the photophase (light period), indicating that the majority of activity occurs during the artificial scotophase (dark period; Supp. Figure 1).

Selectivity index of mice in the summer and fall treatments both failed the Shapiro-Wilk normality test (Summer, $W = 0.8688$, $p < 0.05$; Fall, $W = 0.8442$, $p < 0.05$). Nonparametric analysis via Mann Whitney U test reported a difference approaching significance between selectivity indices in the two treatments ($U = 57$, $p = 0.062$; Figure 3). Linear models of selectivity indices with respect to the total amount of seed consumed in grams had normally distributed residuals (Summer trial, $W = 0.896$, $p > 0.05$, $R^2 = 0.878$, $p < 0.001$; Fall trial, $W = 0.950$, $p > 0.05$, $R^2 = 0.914$, $p < 0.001$; Figure 4). An analysis of covariance (ANCOVA) showed an effect of total consumed, but not an effect of season or an interaction between the two (effect of total consumed, $F_{1,24} = 228.27$, $p < 0.001$; effect of season, $F_{1,24} = 1.320$, $p = 0.262$; interaction, $F_{1,24} = 2.728$, p

= 0.112).

Foraging index of mice in the summer and fall treatment both passed the Shapiro-Wilk normality test (Summer, $W = 0.9253$, $p > 0.05$; Fall, $W = 0.9551$, $p > 0.05$). There was a significant difference in foraging indices when analyzed via Student's t-test ($t = -2.7718$, $df = 25$, $p = 0.010$). Linear models of foraging indices with respect to the total not consumed in grams had normally distributed residuals (Summer trial, $W = 0.958$, $p > 0.05$, $R^2 = 0.5771$, $p = 0.002$; Fall trial, $W = 0.0952$, $p > 0.05$, $R^2 = 0.3255$, $p = 0.033$; Figure 6). An analysis of covariance (ANCOVA) showed an effect of total not consumed, but not an effect of season or an interaction between the two (effect of total not consumed, $F_{1, 24} = 17.69$, $p < 0.001$; effect of season, $F_{1, 24} = 2.188$, $p = 0.1521$; interaction, $F_{1, 24} = 0.114$, $p = 0.7385$).

Discussion

The onset of nocturnal activity for fall trials was significantly later than that of summer trials (Figure 2a); however the offset of nocturnal activity showed no difference between the two treatments (Figure 2b). The forward shift in onset and variability of offset indicates that although some shift is happening, there was not increased activity with an increase in the length of the dark phase as expected. This finding is interesting, because previous research has shown that under experimental seasonal shifts (summer to fall) other small mammals, specifically *Blarina brevicauda* become less strictly nocturnal (Brandt and McCay 2006). Although some activity was observed in the photophase of both summer and fall treatments, there is not substantial evidence from this study to confirm that *P. m. gracilis* undergo the same 'loss of strictly nocturnal activity' during an artificial seasonal shift (Supp. Figure 1). For the purpose of this

experiment, the observed shift during the short 3-day holding period supports the hypothesis that the primacy (immediate) effects of seasonality shifts can be synthesized with this experimental design.

The selectivity for seeds of the genus *Acer* was affected by the brief shift in seasonality. The preference for *A. rubrum* over *A. saccharum* and relationship between preference index and total consumed showed a significant difference between treatments, indicating that *P. m. gracilis* have a stronger preference for *A. saccharum* when exposed to an artificial shift in season. The relationship between amount eaten and preference index showed a non-zero slope, but the relationship did not vary significantly between treatments. This indicates that a relationship exists between preference and amount eaten that is not dependent on seasonal availability of seeds. *P. m. gracilis*'s selectivity for food source may be driven by an underlying evolutionary factor, however hormonal and genetic analysis would be necessary to explain this relationship further.

The foraging behavior for uneaten seeds, defined as seeds that were handled, was affected by the experimental shift. Under an experimental shift in seasonality, the foraging indices indicated a stronger preference for handling *A. saccharum* seeds; however, the lack of a relationship between amount uneaten and foraging indices demonstrates that not all aspects of the complex foraging behaviors of *P. m. gracilis* are affected by brief seasonal shifts. Seeds that were presumably handled by the mice were found in several locations: ranging from inside the polyfill nest to buried in the corn cob bedding. Although it is difficult to quantify 'caching behaviors,' this experiment's definition of 'foraging behaviors' serves as a rudimentary proxy.

Several aspects of this study indicate that further research is necessary to solidify the effects of seasonal shifts on the foraging behavior of *P. m. gracilis*. An increased holding period would ensure that the shift in seasonality is appropriately mimicked, but it is worth noting the unpredictability in seasonality brought on by climate change could be as brief as 3 days. Further analysis would also independently examine the effect photoperiod and temperature on foraging behavior.

Complete analysis of seasonal and circadian rhythms goes far beyond the scope of this study. Seasonal changes in climate have been shown to affect the hypothalamic regulation of food intake and body weight in mammals (Ebling 2015). Further studies should allow for the analysis of genes and hormones associated with rhythmicity and foraging behaviors: genes in the circadian pathway (*i.e.*, CLOCK, BMAL, PERIOD, and TIMELESS) and hormones implicated with feeding behaviors that vary seasonally (*i.e.*, leptin, glucocorticoids, and gonadotropins) could be targets for further analysis (Walton et al., 2011). If manipulation of these genes and hormones could be tied to the behavioral difference observed in this study, it would inform us of the physiological and neurobiological effects that seasonal shifts have on foraging behavior.

The results of this study did support the existence of the primacy effects of shifts in seasonality. Under such stress, *P. m. gracilis* showed an increased selectivity and handling of *A. saccharum* seeds. The shift in foraging behavior caused by the artificial shift in seasonality supports the hypothesis that these behaviors have an underlying seasonal rhythm.

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Appendix

Table 1. *Body Measurements and Rhythmic Period of P. m. gracilis.* Weight, body length, ear length, and period length of each mouse in the study are reported as averages \pm standard error from the mean.

<i>Peromyscus maniculatus gracilis</i>				
Trial	Weight (g)	Body Length (mm)	Ear Length (mm)	Period Length (hr) *
Summer	18.13 \pm 1.846	81.467 \pm 2.117	19.07 \pm 0.073	7.51 \pm 0.024
Fall	18.85 \pm 0.222	82.86 \pm 0.406	19.36 \pm 0.045	7.17 \pm 0.017

*Period length defined by hours of activity between onset and offset

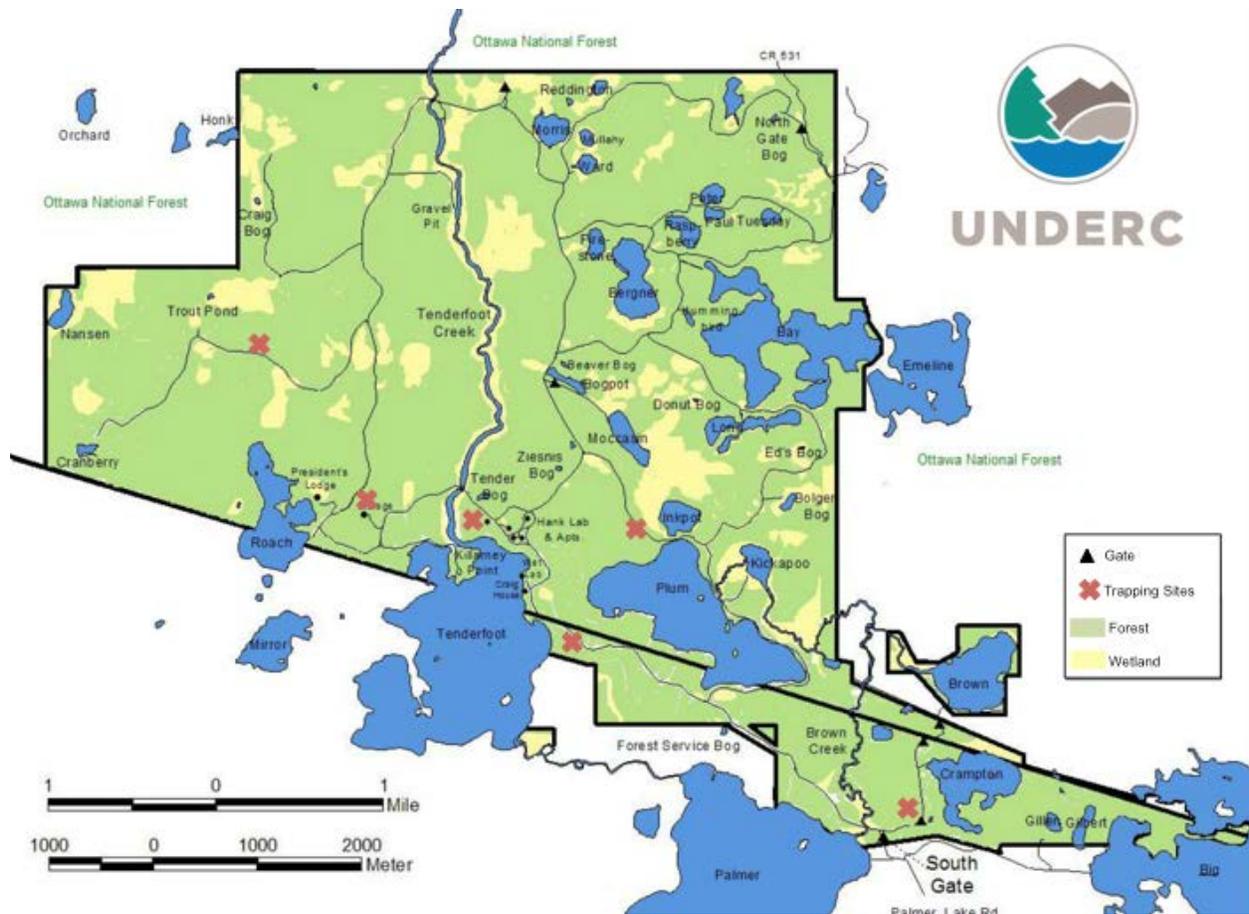


Figure 1. Trapping Sites at the University of Notre Dame Environmental Research Center (UNDERC-East). From May 2016 – July 2016, trapping occurred at six sites dominated by trees of the genus *Acer* in Northern Wisconsin and the Upper Peninsula of Michigan.

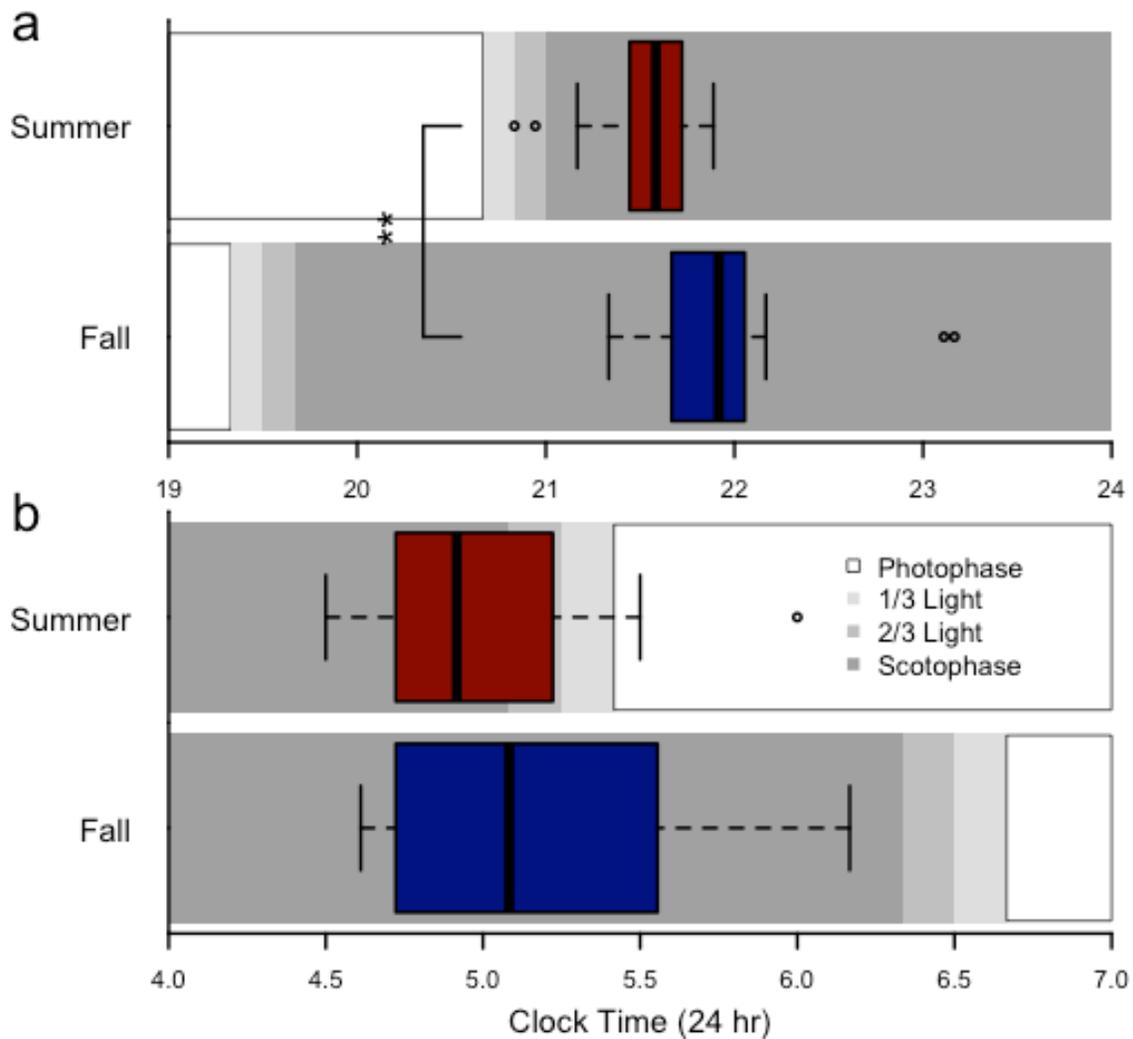


Figure 2. Onset and Offset of Nocturnal Behavior of *P. m. gracilis* under Summer and Fall Conditions. (a) The onset times of mice in the two conditions varied significantly ($W = 33.5, p = 0.003$). (b) The offset times of mice in the two conditions did not vary significantly ($t = -0.9343, df = 26, p > 0.05$).

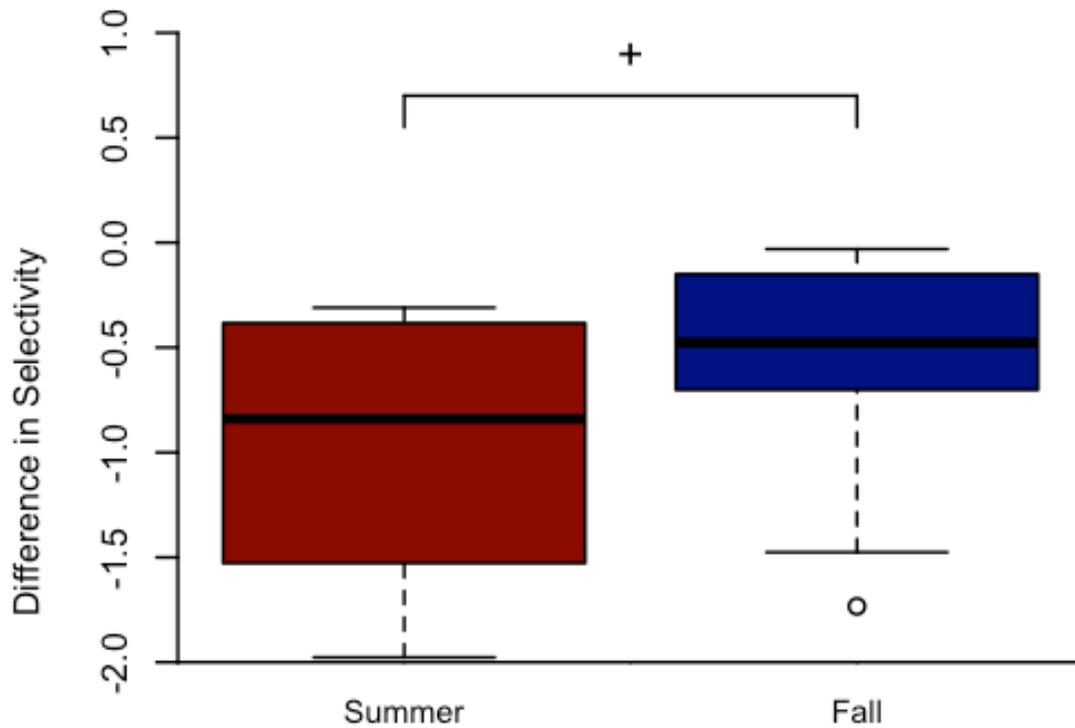


Figure 3. Selectivity Index for Seeds of the Genus *Acer*. The selectivity index was calculated that a score of 2.0 a complete preference for *A. saccharum*, a score of -2.0 indicates a complete preference for *A. rubrum*, and a score of 0 indicates a neutral selectivity ($V = 45$, $p = 0.062$).

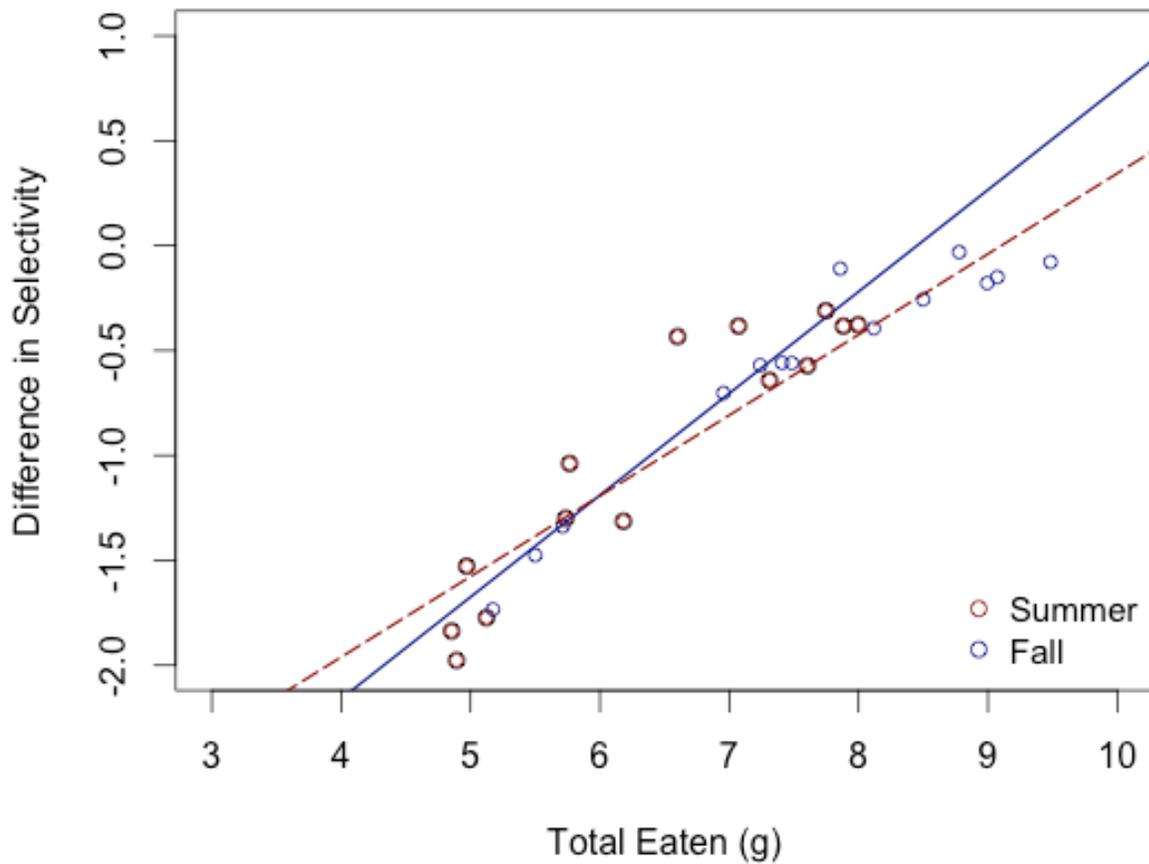


Figure 4. Linear Model of Difference in Selectivity versus Eaten Seeds. Plot of difference in selectivity against total amount eaten with linear regression line for both Summer conditions and Fall conditions. Both conditions demonstrated a positive linear relationship: the difference in selectivity increased with increasing amount eaten (Summer trial (dotted line), $W = 0.896$, $p > 0.05$, $R^2 = 0.878$, $p < 0.001$; Fall trial (solid line), $W = 0.950$, $p > 0.05$, $R^2 = 0.914$, $p < 0.001$).

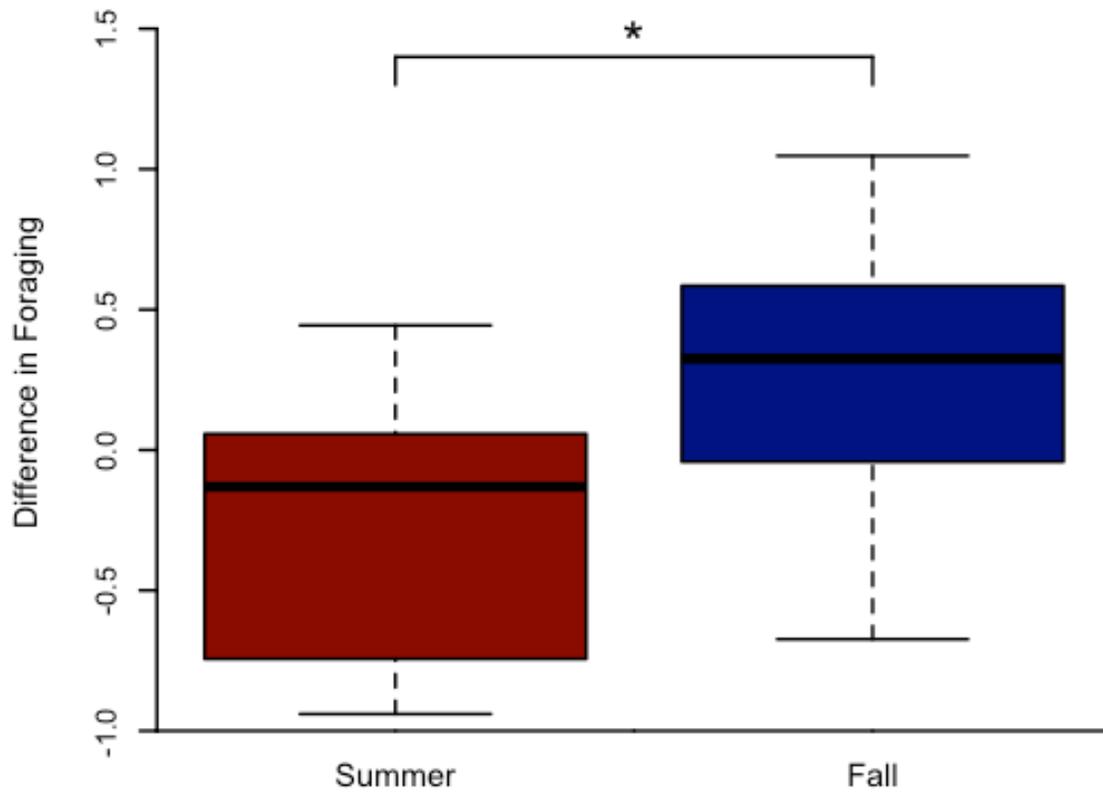


Figure 5. Foraging Index for Seeds of the Genus *Acer*. Uneaten seeds were categorized as either foraged (> 4.1 cm from the seed dish) or not foraged (< 4.1 cm from the seed dish). The foraging index was then calculated that a score of 2.0 indicates that all uneaten *A. saccharum* seeds were foraged, a score of -2.0 indicates that all uneaten *A. rubrum* seeds were foraged, and a score of 0 indicates no preference for species of foraged seeds. Differences between the two trials approached significance ($t = -2.772$, $df = 25$, $p = 0.010$).

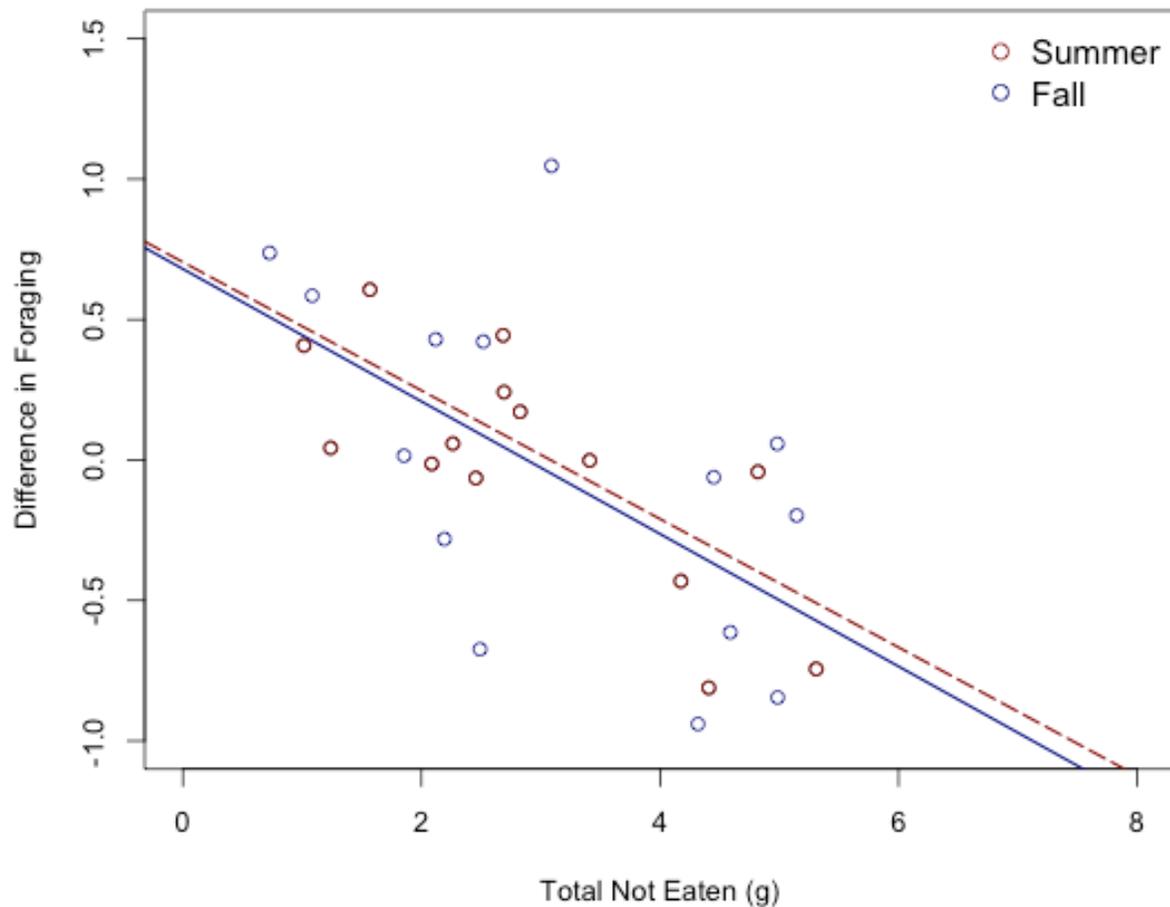
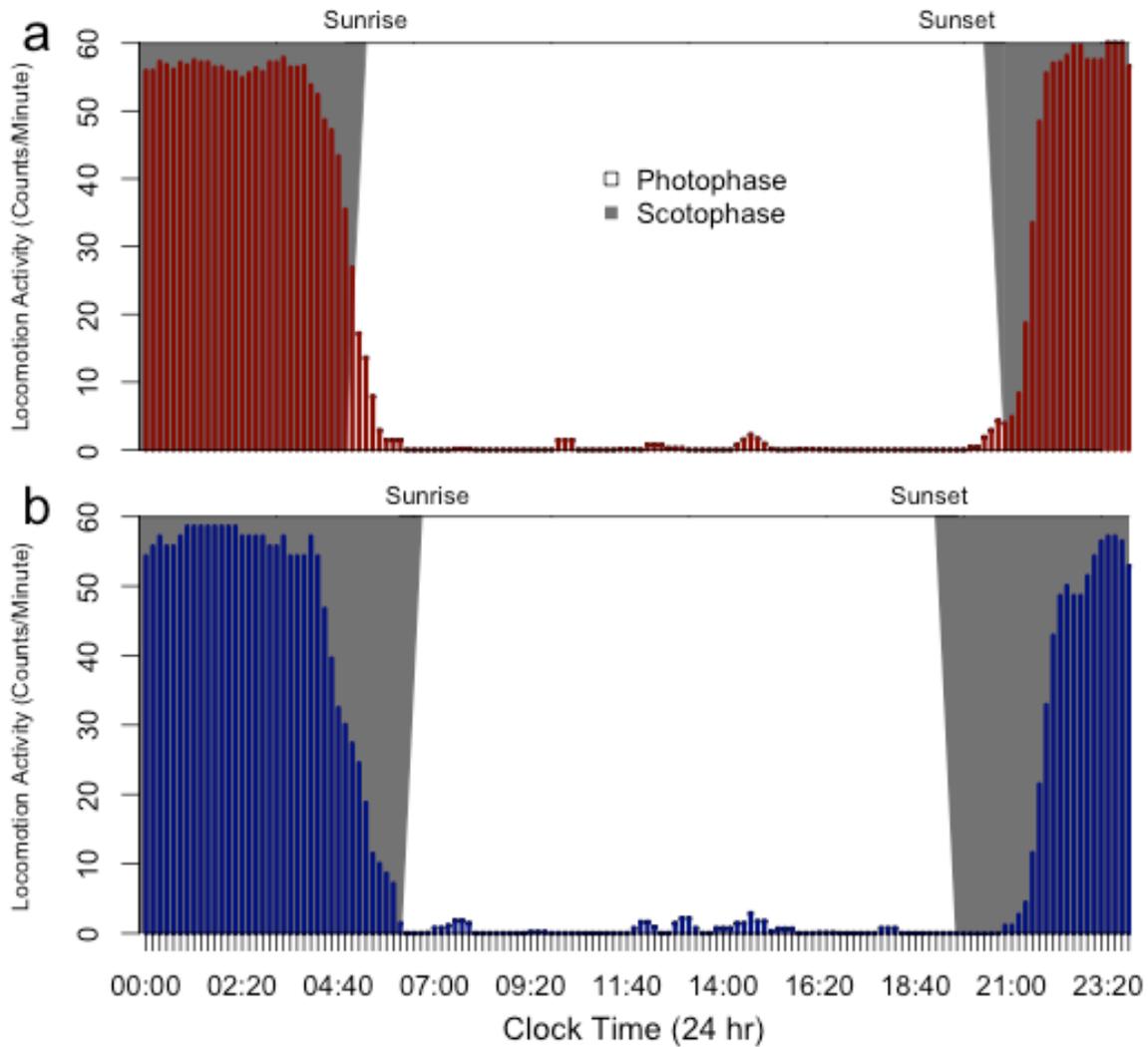


Figure 6. Linear Model of Difference in Foraging versus Uneaten Seeds. Plot of difference in foraging against total amount not eaten with linear regression line for both Summer conditions and Fall conditions. Both conditions demonstrated a negative linear relationship. The difference in foraging decreased with increasing amount uneaten (Summer trial (dotted line), $W = 0.958$, $p > 0.05$, $R^2 = 0.577$, $p = 0.002$; Fall trial (solid line), $W = 0.095$, $p > 0.05$, $R^2 = 0.326$, $p = 0.033$).



Supplemental Figure 1. *Locomotion Activity of P. m. gracilis.* Activity scores were reported in 1-minute bins during the Summer treatment (a, Sunrise 05:00-05:30, Sunset 21:00-21:30) and the Fall treatment (b, Sunrise 06:00-06:30, Sunset 19:20-19:50) every tenth minute from the beginning of the holding period to the beginning of the selectivity trial.