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Environmental Factors' Effects on Eastern Gray Squirrel (Sciurus carolinensis) Infant Populations and Health

Jenny McFarland jennymcfarland17@gmail.com

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ENVIRONMENTAL FACTORS' EFFECTS ON EASTERN GRAY SQUIRREL (*SCURIUS CAROLINENSIS*) INFANT POPULATIONS AND HEALTH

Otterbein University

Department of Biology and Earth Science

Westerville, Ohio 43081

Jenny L. McFarland

16 April 2020

Submitted in partial fulfillment of the requirements for graduation with Honors

Elizabeth (Beaux) Berkeley, Ph. D.

Project Advisor

Andrew Callinger-Yoak, Ph. D.

Second Reader

Erica Van Dop, Ph. D.

Honors Representative

DEPARTMENT OF BIOLOGY AND EARTH SCIENCE

April 22, 2020

1 South Grove Street
Westerville, OH 43081-2006 TEL (614) 823-1517
FAX (614) 823-3042 www.otterbein.edu

Ms. Jenny McFarland cc: Dr. Karen Steigman, Director, Honors Program

Dear Jenny,

With great pleasure, I want to let you know you passed your Honor's thesis defense.

Since we started on this project three years ago, I have been so proud of you and your ability to learn how to do research. From the start you took ownership of this project and ran with it! I have watched you develop new ideas and delve into the literature to justify or eliminate them. As your understanding of your dataset grew, you continued to evaluate new hypotheses and explore new ways of data analysis. I could see your joy in doing the research based on the timestamp of your emails - 30 minutes after I made a suggestion or 11:30 at night, you were thinking about data.

In addition, you pursued multiple opportunities to share your information once you started getting results. I was so pleased that you went after all those grant opportunities at the university, local and national levels. I was even more pleased to see your success at achieving funding! To me this demonstrates your ability to communicate the significance of your project not only to scientists but to a general audience. Other people have noticed this too. I'm thrilled to hear that your project has drawn interest from other professional wildlife biologists. Hopefully we can collaborate on a larger project to expand use of the data you have collected and analyzed.

All in all, an excellent effort! You have so many talents and scientific aptitude and I wish you all the best in your future career and education endeavors.

Best regards,

Elzabeth V. Berkley

Elizabeth (Beaux) V. Berkeley, PhD Assistant Professor Email: eberkeley@otterbein.edu

Environmental Factors' Effects on Eastern Gray Squirrel (*Sciurus carolinensis*) Infant Population Numbers and Health

Jenny McFarland¹, jenny.mcfarland@otterbein.edu

Beaux Berkeley¹, eberkeley@otterbein.edu

Stormy Gibson², sgibson@ohiowildlifecenter.org

¹Otterbein University Department of Biology and Earth Science, 1 S Grove St Westerville, OH 43081

2Ohio Wildlife Center Administration Office, 6131 Cook Rd Powell, OH 43065

Table of Contents

Abstract: Ecosystem factors, both biotic and abiotic, impact all animal species. Temperature, rainfall, daylight, windspeed, mast production, competition and predation are integral to the ecosystem and thus affect the survival and overall wellbeing of the population. Eastern gray squirrel (*Sciurus carolinensis*) infant intakes at Ohio Wildlife Center followed a pattern of more infants in the fall than in the spring, differing from the usual observation that more infants are born in the spring. Ecosystem factors were compared to monthly and annual intakes to see what influenced intake date, admittance condition and survivability rate of the Eastern gray squirrel infants. The results show two birth peaks for Eastern gray squirrels, with over 60% of annual infants admitted during August and September. There were moderate correlations between the infant intake and average monthly temperatures, rainfall, windspeed, mast and aerial predator intake. In general, warmer temperatures correlate to higher infant intakes, which suggests that climate change may impact infant intake. This information will be valuable to wildlife rehabilitation facilities in preparing for spikes of Eastern gray squirrel infant intakes for ordering supplies, recruiting volunteers and asking for donations by allowing them to predict these environmental trends in their geographic region.

Keywords: competition, Eastern gray squirrel, mast production, precipitation, predator-prey relationships, reproduction, survivability, temperature

Introduction

The biotic and abiotic factors of ecosystems provide important resources to animal populations (Marolla et al., 2019). Factors such as weather and climate patterns impact food and resource availability for many species (Ogutu, Piepho, Dublin, Bhola & Reid, 2008; Bionda & Brambilla, 2012; Wallace et al., 2016; Schmidt et al., 2018). Populations may experience fluctuations during surplus or reduced climatic activity (Steele & Smallwood, 1994; Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Bionda & Brambilla, 2012), such as seasonal temperature shifts (Hostetler, Kneip, Van Vuren & Oli, 2014; Schmidt et al., 2018) and varied precipitation rates (Ogutu, Piepho, Dublin, Bhola & Reid, 2008; Hostetler, Kneip, Van Vuren & Oli, 2014; Wallace et al., 2016), which can lead to competition over mast, predation and various female reproductivity rates (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008).

Temperature changes, both seasonal and climatic, impact the activity levels, survival, and behavioral practices of many species (Nixon & McClain, 1969; Koprowski, 1991; Bionda & Brambilla, 2012; Hostetler, Kneip, Van Vuren & Oli, 2014; Wallace et al., 2016; Row & Fedy, 2017; Schmidt et al., 2018; Marolla et al., 2019). Climate change not only effects demographic rates, but also reproduction and survival rates (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Bionda & Brambilla, 2012; Hostetler, Kneip, Van Vuren & Oli, 2014). Temperature fluctuations also effect precipitation such as rain, snow, sleet and hail (Hostetler, Kneip, Van Vuren & Oli, 2014). Precipitation aids populations in providing water to supply food sources (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Ogutu, Piepho, Dublin, Bhola & Reid, 2008; Wallace et al., 2016; Schmidt et al., 2018) which leads to plentiful resources that keep predation in check (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Wallace et al., 2016; Schmidt et al., 2018) and keeps habitats clean from disease (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Bionda & Brambilla, 2012). Precipitation rates influence the success of reproductivity among populations (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Ogutu, Piepho, Dublin, Bhola & Reid, 2008; Bionda & Brambilla, 2012; Hostetler, Kneip, Van Vuren & Oli, 2014; Selonen, Wistbacka & Korpimaki, 2016; Wallace et al., 2016; Charter et al., 2017) as well as the populations' survivability (Ogutu, Piepho, Dublin, Bhola & Reid, 2008; Bionda & Brambilla 2012).

6

Temperature and precipitation are important influences on the growth of mast, or vegetative food resources (Selonen, Wistbacka & Korpimaki, 2016). Mast production, or the total amount of mast produced in annually, is important for animal species that rely on plant matter to survive and occurs in two forms: soft (fleshy fruits) and hard (nuts) (*Mast Tree Network*, 2009*)*. The hard mast production is essential for the survival of squirrel populations, who heavily rely on the production of oak acorns as a part of their food resources, caching, and eventual survival success (Edelman & Koprowski, 2006; Xiao, Gao, Jiang & Zhang, 2009; Selonen & Wistbacka, 2015).

North American squirrel populations use their mast resources for eventual reproductive energy outputs (Nehaus, 2000; Steele & Koprowski, 2001; Dantzer, Boutin, Humphries & McAdams, 2012). The availability of mast influences the survival and reproductive rates of each population (Gurnell, 1987; Steele & Koprowski, 2001; Costello et al 2003; Dantzer, Boutin, Humphries & McAdams, 2012; Selonen & Wistbacka, 2015; Greenburg & Zarnoch 2018). In years when mast is abundant, squirrels have been found spending less time foraging for food or defending mast sites, and spending more time invested in breeding and rearing behaviors (Boutin, Larson & Berteaux, 2000; Steele & Koprowski, 2001; Parker, Gonzales & Nilon, 2014; Prince, DePerno, Gardner & Moorman, 2014). Female squirrels with high body conditions due to plentiful mast have noted to lactate more (Nehaus, 2000; Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008) and have larger litter sizes (Nehaus, 2000; Edelman & Koprowski, 2006).

In years of low mast, competition and predation becomes present as different species fight for highly valued resources (Dantzer, Boutin, Humphries & McAdam, 2012; Lamontagne et al., 2013). In competition, members of the same species compete for their ideal mast, causing bigger and/or more experienced individuals to have more mast acquired, bigger territories, and produce more offspring (Steele & Smallwood, 2004; Parker & Nilon, 2008; Dantzer, Boutin, Humphries & McAdam, 2012; Lamontagne et al., 2013). Weaker individuals or those less experienced are left with fewer resources and low-quality mast (Lamontagne et al., 2013; Freeman & Bachman, 2016). In species of a similar trophic level, they learn to coexist either by creating niches of the desired masts or having population cycles that are non-correlative (Smith & Follmer, 1972; Dueser & Shugart, 1978; Glass & Slade, 1980; Gohen & Swihart 2003; Prince, DePerno, Gardner & Moorman, 2014; Mazzamuto, Bisi, Wauters, Preatoni & Martinoli, 2017). When full competition is present, decreases occur in population densities, reproductivity rates and survival rates (Mazzamuto, Bisi, Wauters, Preatoni & Martinoli, 2017).

Predation affects the survival of the predator species (O'Dongohue, Boutin, Krebs & Hofer, 1997; Kamler, Ballard & Wallace, 2007; Schmidt et al., 2018; Jokinen, Hanski, Numminen, Valkama & Selonen, 2019). Predator population cycles follow those of their prey in order to provide ample amounts of food resources to promote successful survival rates (O'Dongohue, Boutin, Krebs & Hofer, 1997; Kamler, Ballard & Wallace, 2007; Leon-Ortega, Mar Delgado, Martinez, Penteriani & Calvo, 2016; Schmidt et al., 2018). Predator and prey species can change their mast and food resources due to a change in resource quality or abundance, usually in accordance to the present population cycle interactions (Kamler, Ballard & Wallace, 2007; Kozlowski, Gese & Arjo, 2008; Leon-Ortega, Mar Delgado, Martinez, Penteriani & Calvo, 2016; Wallace et al., 2016; Schmidt et al., 2018).

The population cycle of many species relies on many aspects of weather, competition, and food availability (Steele & Koprowski, 2001; Row & Fedy, 2017). The success of each population cycle relies on the reproductive rates of the population and the survival of its offspring (Row & Fedy, 2017). Cycles in rodent species rely on many environmental factors (Steele & Smallwood, 1994; Choquenot & Ruscoe, 2000), and with shorter gestation periods (44 days for squirrels), they are easier to monitor for longer lengths of time (Sharpe & Sherrill, 2017). In squirrels, there is a 50-70% mortality rate in the first year, which increases in their second year (Mosby, 1969; Barkalow, Hamilton & Soots, 1970; Thompson, 1978; Sharpe & Sherrill, 2017). This short life span and high mortality rate makes it easier to follow an individual for its whole life (Steele & Koprowski, 2001).

The Eastern gray squirrel (*Sciurus carolinensis)* (abbreviated as EGS throughout) experiences two reproductive seasons in North America (Pokines, Santana, Heller & Price, 2016), one between approximately March-early May (Brown and Yeager 1945; Moore 1957) and one between approximately August-mid September. This allows for two reproductive cycles to be studied in one year. However, it has previously been shown that most females do not reproduce more than once per year (Steele & Koprowski, 2001) and with gestation being 44 days and adulthood being reached between 9-11 months (Webley & Johnson, 1982; Steele & Koprowski, 2001), some females have spring litters and some females have fall litters. Based on the interaction of mast and adult fitness, it has been assumed that more mast and better adult fitness leads to larger squirrel litter sizes and higher survivability rates (Fox, 1981). However, it is currently believed that weather patterns and predation do not impact the survival of juvenile squirrels (Allen, 1982; Hansen & Nixon, 1986; Thompson, 1978; Steele & Koprowski, 2001) and little research has been done comparing competition and survivability (Steele & Koprowski,

2001). With many open ends of how EGS infants and populations are impacted by different ecosystem factors, it is hypothesized that weather, mast production, competitor populations and predator populations influence EGS infant population numbers and health. Therefore, it is predicted that: 1) higher amounts of produced mast will lead to more EGS offspring, 2) increased temperatures, rainfall and daylight will lead to more EGS offspring, 3) lower windspeeds will lead to healthier EGS offspring, 4) more predators will correlate with more EGS offspring populations and 5) more competitors will correlate with more EGS offspring populations.

Methodology

The collection of EGS admission dates, admission health conditions, reason for admission and outcomes (released or deceased) have been provided by Ohio Wildlife Center (abbreviated as OWC throughout). The OWC is a nonprofit wildlife hospital, rehabilitation facility and education center in Dublin, Ohio. Their records are kept for all admitted wildlife, noting their species, age, admission condition, location of intake and their outcome. The annual, monthly and average monthly EGS infant admission numbers were calculated by the SUM and AVERAGE features on Microsoft Excel. To calculate the percent of annual admissions, (specific month total/annual total) *100 was used in Microsoft Excel. Bar graphs were created through Microsoft Excel to make comparisons within EGS subgroups, such as Clinically Healthy versus Unhealthy admissions. Bar graphs were given error bars, which represent standard deviation throughout. Standard deviation was calculated through the STDEV feature on Microsoft Excel. When standard error was utilized, the formula STDEV(specific values)/SQRT(COUNT(specific values)) was used. "X" and "Y" labels represent significance in data (p≤0.05).

The OWC database was also used to collect the data on red squirrels, red-tailed hawks, red foxes, great horned owls, barred owls, barn owls, eastern screech owls and snowy owls. The data for all owl subspecies was combined, as there weren't as many owl admissions to the hospital between 2013-2018 compared to the other species. The (specific month total/annual total) *100 formula was used to calculate the percent of annual admissions for all species; these results were correlated against the EGS infant percent of annual admissions in scatter plots on Microsoft Excel. A linear trendline was set and an $R²$ value was selected to be visible on the scatter plot. Throughout the project, R^2 values ≥0.6 were considered to designate a high

correlation, $0.3 \ge R^2 > 0.6$ a moderate correlation, $0.1 \ge R^2 > 0.3$ a low correlation, and <0.1 was no correlation.

All weather data (temperature, rainfall, windspeed and daylight hours) were taken from the National Weather Service weather history website, with a specific location set to collect information from the John Glenn International Airport in Columbus, Ohio, USA (40 °N, 82.89) ⁰W). The database was used to collect the monthly average for each weather specificity on their history database, so the average was not calculated in Microsoft Excel. Rainfall was denoted rather than total precipitation to exclude snowfall and sleet. These monthly averages were correlated against the EGS infant percent of annual admissions in scatter plots on Microsoft Excel. A linear trendline was set and an R^2 value was selected to be visible on the scatter plot.

The mast production data was from the Ohio Department of Natural Resources (ODNR) annual acorn mast report for the state of Ohio 2013-2018. Since the OWC mainly serves the greater Columbus area, only mast sites within ODNR District 1 were used to calculate data (n=4). These sites were Big Island, Kokosing, Delaware and Deer Creek. The annual percentage of white oaks and red oaks producing at each site were used to create an annual average [(white oak percentage+ red oak percentage)/2]. This average was correlated against the EGS infant admissions data in scatter plots on Microsoft Excel, which then had a linear trendline and $R²$ value to plot the correlation.

EGS infant admission conditions were grouped into 5 subcategories: Clinically Healthy, Undetermined/DOA, Internal Problems, External Problems and Malnourished/Dehydrated. Clinically Healthy denotes that the EGS infant appears healthy upon examination, and that the volunteer admitting the animal can see no injury or malnutrition. Undetermined is listed if the volunteer notices something wrong with the EGS infant but does not know what specifically and does not feel confident listing the EGS infant under any other admission category, while DOA stands for "dead on arrival". Internal Problems was a group made to describe any internal issue that effects the EGS infant's wellbeing and was the following admission conditions: "nervous system problem", "digestive system problem", "musculoskeletal system problem", "hypothermia" and "depression/lethargy". External Problems was a group made to describe any external issue that effects the EGS infant's wellbeing and was "integumentary/skin problems" and "ocular/eye problems". Malnourished/Dehydrated was a group to combine "generalized/thin/loss of body condition" and "generalized/dehydrated".

Results

Of the studied 2013-2018 EGS infant data, there were two seasonal intake peaks (Figure 1). August (which had both the highest average admissions for the fall peak but also the most admissions annually) accounted for 40.78% of the average annual admissions, while April (the spring peak) accounted for 16.88% of the average annual admissions (Figure 1). However, the April peak still doesn't represent the second highest intake month on average, as September has an average intake of 21.88% of the annual admissions (Figure 1).

For total EGS infant annual admissions, 2017 had the highest admissions for EGS infants of 469 and 2018 had the lowest admissions of 281 (Figure 2). Admissions in 2017 were significantly different (p=0.030876) from admissions in 2015 and 2018, but no other years were significant from each other (Figure 2).

Figure 2: EGS infant admissions to the OWC from 2013-2018. Error bars represent standard deviation (±67.917).

While annual admissions did not show many significant differences, admissions were significantly different for all January-June and July-December seasons (Figure 3). As before mentioned in Figure 1, the August peak greatly influenced the amount of annual admissions for the fall season, which made up for over 60% of annual admissions each year (Figure 3).

Figure 3: Percentage of EGS infant admissions for the January-June and July-December seasons. Error bars show standard deviation (±7.115139). Significance was found between all January-June and July-December seasons annually (p=0.00000453, denoted as X).

No trend was found between the amount of EGS infants that were released back into the wild or that died before the opportunity for release (made up of the total for those that died in care, were dead at the time of arrival, were euthanized in care or were euthanized at the time of arrival). More EGS infants were released in 2014-2018 (Figure 4); however, only 2016-2018 had significantly more infants released than died in care (Figure 4).

There was variation found between the survivability of the EGS infants and the conditions upon their admission. Significantly more EGS infants that were Clinically Healthy were released than died or were euthanized. (Figure 5). Significantly more EGS infants that had either Internal or External problems were non-releasable (Figure 5).

Figure 5: Average EGS infant admittance conditions and their outcome (whether the infant was released or died/was euthanized). Error bars represent standard deviation (±14.887). Significance (p=0.000000001) was found between the outcomes of Clinically Healthy infants (denoted as X) and for Internal/External Problem infants (denoted as Y).

While comparing the survival of different admission conditions is helpful, comparing the health on a wider scale of the infants is more beneficial to wildlife rehabilitation facilities. For seasons between January-June 2013 to July-December 2016, Clinically Healthy and Unhealthy admission percentages were not significantly different (Figure 6). For all seasons in 2017 and 2018 the admission percentages were significantly different for Clinically Healthy and Unhealthy admissions, showing significantly more Unhealthy admits than Clinically Healthy (Figure 6). On average, there was only significantly more of the Unhealthy admits during the months of July and October (Figure 7).

Figure 6: Percent of seasonal (J-J being January-June and J-D being July-December) EGS infant admissions of Clinically Healthy and summed Unhealthy individuals. Error bars represent standard deviation (±16.084). Significant differences (p=0.0107) were found for every season between J-J 2017 and J-D 2018 (denoted as X).

■Healthy ■Unhealthy

Figure 7: Number of monthly EGS infant admissions that were deemed Clinically Healthy or summed under Unhealthy. Error bars represent standard deviation per month. Significant differences were found between the Clinically Healthy and Unhealthy admissions of July (p=0.0339) and October (0.0411).

Since EGS have two birthing seasons, seasonal variation may influence infant numbers and conditions. Seasonal weather can be measured by temperature (°F), rainfall (inches), windspeed (mph) and daylight (hours). Moderate correlations (0.6>R²>0.3) were found for comparing the EGS infant admissions with the monthly average temperature (Figure 8) and windspeed (Figure 10), but not for daylight hours (Figure 11) or rainfall (R^2 =0.1317). When testing for a correlation between the EGS infant admissions with the pre-monthly weather averages (for example, comparing the April EGS infant admission rates with the March rainfall), a moderate correlation was found between EGS infant admission rates and rainfall (Figure 9), but not for any other weather measurements (R^2 =0.2929 for daylight hours, R^2 =0.2094 for temperature and R^2 =0.1517 for windspeed).

Figure 8: Comparison of average EGS infant admissions per month versus the average monthly temperature (\degree F). R 2 =0.3109.

Figure 9: Average monthly EGS intake compared to the average monthly rainfall (inches) for the month prior.

 $R^2 = 0.4254$.

Figure 10: The average monthly windspeed (mph) compared to the average monthly EGS infant intake. R^2 =0.3159.

Figure 11: The average monthly daylight hours compared to the average monthly EGS infant admissions. R^2 =0.1985.

Oak acorns are one of the main food sources of EGS and their reproduction depends on available seasonal resources. It was found that annually, there was a moderate $(0.6 > R² > 0.3)$ correlation between the annual EGS infant intake and the percentage of oaks producing acorns in the greater Columbus area (Figure 12).

Figure 12: Average (%) of white and red oaks producing acorns annually in ODNR District 1 compared to the annual number of admitted EGS infants. $R^2 = 0.5206$.

The seasonal weather and mast production level has some effects on the situations that leads to why EGS infants are brought into OWC's hospital and what condition the infants are in upon arrival. Orphans/ Parents Not Available had the highest number of correlative factors, with 3 moderate correlations and 1 high correlation with environmental factors (Table 1). Nervous system problems had 3 moderate correlations (Table 2), which was the most of any admission condition.

Table 1: The average monthly situations of EGS infant admission and the R² correlation values against the average monthly temperature, rainfall, windspeed, daylight hours and mast production. Negative R² values designate a negative correlation and positive R^2 values designate a positive correlation value. R^2 values <0.1 are not correlative, 0.1-0.3 are a low correlation, 0.3-0.6 are a moderate correlation and 0.6-1 are a high correlation. Values in bold show a moderate or high correlation.

Table 2: The average monthly health conditions of EGS infants at admission and the $R²$ correlation values against the average monthly temperature, rainfall, windspeed, daylight hours and mast production. Negative R² values designate a negative correlation and positive R^2 values designate a positive correlation value. R^2 values <0.1 are not correlative, 0.1-0.3 are a low correlation, 0.3-0.6 are a moderate correlation and 0.6-1 are a high correlation. Values in bold show a moderate or high correlation.

EGS infant intraspecific competitors (juveniles and adults) are also frequent visitors to the OWC, but do not make up over 200 individuals annually (Figure 13). Annually, there were significantly more EGS infants admitted than juveniles or adults (Figure 13).

Figure 13: Comparison of EGS infants admitted annually and their intraspecific competitors: EGS juveniles and EGS adults. Error bars represent standard deviation (±67.91073 for infants, ±33.600099 for juveniles and ±15.466092 for adults). Significance was found annually when comparing the number of infants admitted to the number of juveniles $(p=0.0000237,$ designated as X) and the number of adults $(p=0.0000564,$ designated as Y).

Competition with other animals for resources can also impact the survival of EGS infants, specifically with other squirrels that share similar shelters, food sources and territories. Red squirrels, for example, share similar habitats in central Ohio with EGS and also experience the bi-annual birthing seasons. However, there is a low correlation (0.1 $<$ R² $<$ 0.3) between the EGS infant admissions and the red squirrel infant admissions (Figure 14).

Figure 14: Average EGS and red squirrel monthly infant admissions $%$. R²=0.2119.

The number of predators in the area may also determines the health of the EGS infants. It was found that there is a moderate $(0.6 \times R^2 > 0.3)$ correlation between the EGS infant admissions and both the red-tailed hawk (Figure 15) and owl (Figure 16) admissions. No correlation $(R^2<0.1)$ was found between EGS infant admissions and red fox (Figure 17) admissions.

Figure 15: Predator-prey comparison of EGS infant admissions and red-tailed hawk admissions. R^2 = 0.4625.

Figure 16: Predator-prey comparison for EGS infants and for combined owl admissions. $R²=0.3133$.

Figure 17: Predator-prey relationship between EGS infant admissions and red fox admissions. $R²=0.0049$.

Discussion

In total there were 2,188 EGS infants admitted to the OWC's hospital between 2013- 2018. There were 469 admitted in 2017 (which was the largest admission year) and the 281 admitted in 2018 was the lowest admission year (Figure 2). Despite variation in EGS infant admissions annually, August was consistently the month of highest admissions with an average of 40.78% of all annual infants being admitted (Figure 1). August also represented the peak of the fall admissions, with April representing the peak of the spring admissions with an average of 16.88% of the annual admissions (Figure 1). Admissions were relatively low between these two peaks (excluding September, which almost acted as an overflow of EGS infants). The EGS infant intake significantly exceeded the intakes of EGS juveniles and EGS adults annually (Figure 13). This is likely due to being an r-selected animal (having many babies to compensate for a short lifespan). EGS populations, along with other rodents, commonly experience cycling based on timing between reproductive success and resource availability (Gurnell, 1987; Steele & Smallwood, 1994; O'Dongohue et al., 1997; Choquenot & Ruscoe, 2000; Steele & Koprowski, 2001; Row & Fedy, 2017). Populations increase when there is a large amount of available resources, low mortality rates, high reproduction success rates, high survivability rates, and immigration (alternatively, populations decrease when the opposite is present) (Barkalow, 1967; Mosby, 1969; Thompson, 1978; Hansen et al., 1986; Row & Fedy, 2017). There is an almost 50% mortality rate for EGS under 1 year of age, so EGS adults made up the fewest number of intakes annually (Figure 13).

When dividing the EGS infant admissions by January-June and July-December, there were 679 admitted in January-June and 1,509 admitted in July-December (Figure 3). The July-December admissions annually make up 60.85-79.45% of the total admissions (Figure 3). Having this many admissions of infants may demonstrate that the spring mast and resources allowed for EGS mothers to have a successful breeding season, gestation and birth. EGS infant gestation is approximately 45 days, and with June admissions being relatively low (Figure 1), this could mean that females are investing more time into finding mates and food rather than raising young at this time.

There is little trend present in the annual percentage of the EGS infants that are released versus the ones that die in care (Figure 4). The annual percentage for "died/euthanized" includes all EGS infants that were dead upon arrival, died naturally in care, were euthanized upon arrival and were euthanized in care. This means that this graph represents both natural and unnatural deaths; however, as much as possible, the OWC makes euthanasia decisions that are in the benefit of the EGS infant to prevent extended pain and a low quality of life. When breaking up the annual EGS infant admissions into four larger categories (Clinically Healthy, Malnourished/Dehydrated, Internal Problems and External Problems), there are significantly more Clinically Healthy infants released while on average there are more Malnourished/Dehydrated, Internal Problems and External Problems that died/ were euthanized (Figure 5). This brings an ethical question to wildlife rehabilitation facilities: should there be a higher investment into the Clinically Healthy admitted EGS infants that are more likely to be released than infants with any physical problems?

Malnutrition and dehydration may be caused by EGS infants relying on soft mast and being unprepared once those resources are used and hard mast becomes the only available resource (Steele & Koprowski, 2001; Selonen, Wistbacka & Korpimaki, 2016). These health problems may also be the result for infants of the fall birthing season as they have had less time to cache and add body mass compared to infants from the spring birthing season (Steele & Koprowski, 2001; Selonen & Wistbacka, 2015; Selonen, Wistbacka & Korpimaki, 2016). Internal and External problems can be caused by a variety of cases, such as parasites (in which EGSs are known to susceptible to 104 species) (Koprowski, 1994), falls, human interactions, electricity shocks, dog encounters, cat encounters, escapes from predators, etc. (Steele & Koprowski, 2001). When the Malnourished/Dehydrated, Internal Problems and External Problems are grouped into an Unhealthy category and compared with the Clinically Healthy admissions, there is little difference between the January-June and July-December EGS infant admissions

between 2013-2016 (Figure 6). However, 2017 and 2018 had significantly more Unhealthy admissions than Clinically Healthy admissions, including the July-December season of 2017 which had 88.75% of its admissions be Unhealthy EGS infants (Figure 6). When comparing the average of annual Clinically Healthy and Unhealthy admissions by month, August has both the highest intake of Clinically Health and Unhealthy admissions (Figure 7). This is likely due to August having the highest amount of admissions per year (Figure 1). Only May and October had significantly more Unhealthy EGS infant admissions, while no months had significantly more Clinically Healthy infants (Figure 7).

Aspects of the weather impact the amount of resources available to all animal species, including food, water, and shelter. When focusing on temperature $(°F)$, rainfall (inches), windspeed (mph) and daylight (hours), these factors can impact the EGS infants' health conditions and when they are being born. Warmer temperatures allow mothers to be out searching for food and mates more, while also cueing trees and plants to begin producing mast. For example, increased temperatures in July allows for favorable temperatures in which plants produce mast, such as deciduous fruits, acorns and walnuts (Hostetler, Kneip, Van Vuren & Oli, 2014; Row & Fedy, 2017; Schmidt et al., 2018). Increased rain allows for more resources to go into mast producing plants, allowing for more mast to be made (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Ogutu, Pieplo, Dublin, Bhola & Reid, 2008; Bionda & Brambilla, 2012; Hostetler, Kneip, Van Vuren & Oli, 2014; Leitner & Leitner, 2017), as well as creating natural drinking areas. Daylight determines how long these crepuscular animals are active for, as well as how much sunlight energy plants can utilize for photosynthesis.

While these factors can be beneficial, they can also be detrimental to infants. Temperature extremes can cause dehydration or hypothermia. Lack of rain can also cause dehydration, while excess rain may cause local flooding and difficulty reaching certain shelters or mast areas. Infants that are ill prepared for shorter days into the fall and winter may be lacking in their cache amount and may begin to become malnourished. Lastly, windspeed can destroy squirrel nests, knocking young out of trees at large heights. Moderate correlations were found between the monthly percent of annual infants admitted and both the average monthly temperature and the average monthly windspeed (Figures 8 and 10). Consideration must also be taken for the month prior to the infants' births, when the mother is gestating them. There was a moderate correlation found between the monthly percent of annual infants admitted and the average monthly rainfall in the month prior to the infants' admission (Figure 9). Low correlations

were found when considering the daylight of the infants' admissions and the month prior to their admissions (Figure 11).

Available mast is often determined by the surrounding climate (Selonen, Wistbacka & Korpimaki, 2016). Weather conditions, such as temperature and precipitation, impact how much mast produced, determining how many resources there are available for a population's survival (Selonen, Wistbacka & Korpimaki, 2016; Wallace et al., 2016; Leitner & Leitner, 2017; Schmidt et al., 2018). Mast requires healthy amounts of water, sunlight and carbon dioxide in order to create the food for many animals, including EGS infants. The EGS diet is made up of a lot of tree mast, both soft (fruits) and hard (nuts). Soft mast is available in the late spring and early summer, such as mulberries and hackberries (Korschgen, 1981; Steele & Weigl, 1992; Steele & Koprowski, 2001). Many EGS will utilize soft masts as a low-output energy food source (meaning that it does not take much time to eat or get to the edible portion of the mast) (Steele & Koprowski, 2001). These resources are eagerly used by EGS who have been using their hard mast reserves from the previous fall. Soft mast is used from June until late July when hard masts will begin to be available, such as black walnuts and oak acorns (Steele & Koprowski, 2001). Soft masts are used by EGS infants born in the spring season to obtain a healthy mass to survive the future lack of food and potentially harsh winters (Selonen, Wistbacka & Korpimaki, 2016).

Hard masts are more time intensive in order to reach the edible portion of the seed, and juveniles either do not know how to open hard mast seeds or they continue to search for soft mast to no avail (Steele & Koprowski, 2001; Selonen, Wistbacka & Korpimaki, 2016). Some infants and juveniles haven't developed fully in order to utilize these resources (such as having underdeveloped teeth to break through nut shells, or are still too small to carry the large hard mast to a safe eating area) (Korschgen, 1981; Steele & Weigl, 1992; Selonen, Wistbacka & Korpimaki, 2016). EGS, unlike other squirrels, also have an additional set of premolars, which may not be fully developed when extremely young infants are in search of hard mast (Steele & Koprowski, 2001). For EGS infants born in the fall, they also lack enough time to build upon their fat reserves for the winter and enough time to build caches to survive the whole winter (Selonen, Wistbacka & Korpimaki, 2016). In fall, squirrels must eat approximately 32% more food than is required for their daily intake in order to build up their winter masses (Ludwick, Fontenot & Mosby, 1969). In other cases, the mother EGS is having trouble locating high quality hard mast to be able to make milk necessary for her infants (Steele & Koprowski, 2001). Frosts also impact what resources are available, as large and late frosts can decimate soft mast

production, creating a low food resource reserve for a growing population (Nixon & McClain, 1969; Koprowski, 1991; Steele & Koprowski, 2001).

Oak acorns are utilized by EGS, as the edible portions are easily reached, are found in mass numbers at one time, and they are a small, transportable size back to a winter cache (Korschgen, 1981; Steele & Weigl 1992). The two most common oaks, white and red, are both found in central Ohio. Red oak acorns have a high fat content, making them better for cache storage for the winter, as they will decay at a slower rate, have a later germination date, and the higher fat content can be used by EGS to utilize for their body mass in the winter (Steele & Koprowski, 2001; Apsley & Gerht, 2016). White oak acorns have a lower fat content and are eaten more in the fall season to allocate for greater body mass rather than for storage (Steele & Koprowski, 2001; Apsley & Gerht, 2016). There was a moderate correlation found between the annual number of EGS infants admitted and the annual average of white oaks and red oaks producing acorns in the central Ohio area (Figure 12). This is consistent with the findings that temperature and rainfall also moderately correlate to EGS infant admissions, since mast is dependent on these two factors for growth and stimulus.

Once resources run out, usually depending on the mast available, the population decreases until the resources can support a population increase (Steele & Smallwood, 1994; O'Dongohue et al., 1997; Dantzer et al., 2012; Row & Fedy, 2017; Schmidt et al., 2018). Mast is crucially important for a thriving population and has the highest correlation between any of the test environmental factors to the EGS infant admissions. While all of the data given from the ODNR about the oak acorn production was given annually, the acorn availability by month would also be of use to support the data, which would better support the peak in admissions in August if there was an acorn peak in June or July. This would lead to the insinuation that females would have more mast available to eat, allowing for healthier, larger, and/or more EGS infants to be born (Nehaus, 2000; Costello, Jones, Inman, Inman, Thompson & Quigley, 2003; Edelman & Koprowski, 2006; Parker, Gonzales & Nilon,2014; Selonen & Wistbacka, 2015), and for the infants to have healthier mothers to provide more milk (Nehaus, 2000; Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008).

The five tested environmental factors (temperature, rainfall, windspeed, daylight and mast) all have different implications as to why the infants were brought to the hospital, as well as what health conditions they were brought in with. Both mast and daylight correlated with 4 out of 10 of the admission situations, with three high correlations between mast/Behavioral Stranding, mast/Entrapment and daylight/Orphans (Table 1). Meanwhile, Orphans were

moderately correlative with 3 out of 5 environmental factors and highly correlative with 1 out of 5 environmental factors (Table 1), suggesting that orphans are influenced the most by the weather and mast production in comparison to other infants. For admission health conditions, both mast and temperature were moderately correlative with 3 out of 10 of the health conditions (Table 2). Nervous system problems were the most correlative health condition, with moderate correlations to 3 out of 5 environmental factors (Table 2).

When comparing the EGS infant admissions to that of their competitors and predators, there were moderate correlations found with aerial predators (Figures 15 and 16) but not correlative with their terrestrial predator (Figure 17) and had a low correlation with their competitor (Figure 14). This is concise with the fact that EGS are tree-dwellers and would have a greater likelihood of encountering an aerial predator than a terrestrial predator. Foraging more often means that there is an increased risk of predation (Jokinen, Hanski, Numminen, Valkama & Selonen, 2019). EGS infants who have also left the nest may also be too focused on obtaining mast to notice potential ambush predators; this leaves infants vulnerable while searching for food. Young squirrels are also noted to hide more often to scan areas of mast, which sometimes leaves them vulnerable from predators that they do not expect (Freeman & Bachman, 2016). While EGS have an ideal coloration for camouflage against trees and have nimble legs for climbing, on the ground they are more at risk due to their size, especially infants and juveniles, and do not have the leg shape to allow for agile running (Freeman & Bachman, 2016; Sharpe & Sherill, 2017). Aerial predators, such as red-tailed hawks and owls, can easily swoop down from trees and catch unsuspecting or injured EGSs (Koprowski, 1994; Steele & Koprowski, 2001; Leon-Ortega, Mar Delgado, Martinez, Penteriani & Calvo, 2016; Wallace et al., 2016), which would support the moderate correlation of coinciding aerial predator and EGS populations. Terrestrial predators, such as coyotes and red foxes, can ambush EGS while they are foraging on the ground (Koprowski, 1994; Steele & Koprowski, 2001; Kamler, Ballard & Wallace, 2007; Kozlowski, Gese & Arjo, 2008). Coyotes were initially considered for this study due to previous findings that their populations were correlated to that of their prey (O'Dongohue, Boutin, Krebs & Hofer, 1997; Kamler, Ballard & Wallace, 2007; Kozlowski, Gese & Arjo, 2008), but were voided from the study as the OWC is not allowed to admit them. This would be a great opportunity for a future study to include them, as well as domestic terrestrial predators such as cats and dogs, to the study.

As for having a low correlation with their competitor's infant numbers, this may mean that either there are enough resources for both species to thrive or that the species have developed

26

niches to live in the same habitats. An increase in temperatures and precipitation increases the available mast, which ultimately leads to larger amounts of competition for high quality and quantity mast (Parker & Nilon, 2008; Dantzer, Boutin, Humphries & McAdam, 2012; Lamontagne et al., 2013), which means that if both squirrel species were to be utilizing the exact same mast and habitats, then one should have a greater reproductive success than the other. Due to the larger size of the EGS, red squirrels are often outcompeted by EGSs (Mazzamuto, Bisi, Wauters, Preatoni & Martinoli, 2017), which does not match our study.

Conclusion

EGS infants face higher mortality rates when compared to adults due to lack of accessible food, competition with stronger EGS individuals and small size for easy targeting by predators (Lima, Morgan-Ernest, Brown, Belgrando & Stenseth, 2008; Ogutu, Piepho, Dublin, Bhola & Reid, 2008; Bionda & Brambilla, 2012; Wallace et al., 2016; Schmidt et al.). Certain ecosystem factors appear to impact the population number and survivability of EGS infants more than others. Moderate support was found that temperature, rainfall, windspeed and mast production are correlative to the number of EGS infants and when they are born. Moderate support was also found that the number of terrestrial predators is correlative to the number of EGS infants admitted. Thus, the predictions concerning mast, temperatures, rainfall, windspeed and predators (aerial) were supported; the predictions concerning daylight, competitors and predators (terrestrial) were not supported.

Specific research should be done on average mast available monthly, in addition to a separation of soft and hard mast varieties. Another topic to be researched is the impact of squirrel hunting on infant populations. In 1982 in Missouri alone, squirrel hunting brought in \$12.5 million in revenue, resulting in the harvest of 2.5 million squirrels (Flyger & Gates, 1982). With so many adults being harvested, this could leave many hundreds of thousands of orphaned infants. Data could be collected, presumably from the ODNR, about approximate annual squirrel harvest. As of August 2019, it is legal to take up to 6 squirrels per day in hunting season, which begins September 1st. Seeing how squirrel harvest impacts the number of infants orphaned could allude to why there is a higher average percentage of admissions in September. Lastly, a new topic of interest could be deforestation. EGS do not handle deforestation or forest fragmentation well, as they prefer to move from tree to tree rather than across open ground

(Steele & Koprowski, 2001). Data could be done on number of EGS infants coming in per county versus the percentage of that county being considered "developed", "residential" or "city".

Overall, the data supports the hypotheses that weather conditions and aerial predators affect the number of EGS infants and their health. This information could be useful for the OWC Hospital and other wildlife clinics in preparation for increased EGS infant intakes. Certain weather patterns may allow hospitals and clinics to be prepared by asking for more donations, prepping enclosures and ordering formulas. Parts of ecosystems are affecting populations more than others, as this study has shown, and it allows for greater consideration to be taken when considering what affects climate change will have on animal populations.

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Works Cited

- 2013 Acorn Mast Survey Results. (2013). *Ohio Department of Natural Resources: DIVISION OF WILDLIFE* 1-7. http://wildlife.ohiodnr.gov/portals/wildlife/pdfs/research/Mast%20Survey%20Results%20 2013.pdf
- 2014 Acorn Mast Survey Results. (2014). *Ohio Department of Natural Resources: DIVISION OF WILDLIFE* 1-7.

28

http://wildlife.ohiodnr.gov/portals/wildlife/pdfs/research/Mast%20Survey%20Results%20 2014.pdf

2015 Acorn Mast Survey Results. (2015). *Ohio Department of Natural Resources: DIVISION OF WILDLIFE* 1-7.

http://wildlife.ohiodnr.gov/portals/wildlife/pdfs/research/2015%20acorn%20mast%20surv ey.pdf

2016 Acorn Mast Survey Results. (2016). *Ohio Department of Natural Resources: DIVISION OF WILDLIFE* 1-8.

http://wildlife.ohiodnr.gov/portals/wildlife/pdfs/research/2016%20acorn%20mast%20surv ey.pdf

2017 Acorn Mast Survey Results. (2017). *Ohio Department of Natural Resources: DIVISION OF WILDLIFE* 1-7.

wildlife.ohiodnr.gov/portals/wildlife/pdfs/research/2017%20acorn%20mast%20survey.pdf

- 2018 Acorn Mast Survey Results. (2018). *Ohio Department of Natural Resources: DIVISION OF WILDLIFE* 1-7. http://wildlife.ohiodnr.gov/portals/wildlife/pdfs/research/2018%20acorn%20mast%20surv ey.pdf
- Allen, D. S. (1982). Social status and survivorship in a population of eastern gray squirrels *(Sciurus carolinensis*) (Doctoral dissertation). Ohio State University, Columbus, OH.
- Acorn Mast Survey Results Show Increase for White, Red Oaks. 2012. *Ohio Department of Natural Resources: DIVISION OF WILDLIFE.* http://wildlife.ohiodnr.gov/stay-informed/news-announcements/post/acornmast-survey-results-show-increase-for-white-red-oaks
- Apsley, D. and Gerht, S. (2016). Enhancing Food (Mast) Production for Woodland Wildlife in Ohio. *Ohioline: The Ohio State University Extension.* https://ohioline.osu.edu/factsheet/f-60
- Barkalow, F. S., Jr., Hamilton, R. B., and Soots, R. F., Jr. (1970). The vital statistics of an unexploited gray squirrel population. *Journal of Wildlife Management 34* (3):489-500.
- Bionda, R. and Brambilla, B. (2012). Rainfall and landscape features affect productivity in an alpine population of Eagle Owl *Bubo bubo. Journal of Ornithology 153* (1)*:*167-171.
- Boutin, S., Larson, K. W., and Berteaux, D. (2000). Anticipatory parental care: acquiring resources for offspring prior to conception. *The Royal Society 267* (1457)*:* 2029- 2035.
- Brown, L. G., and Yeager, L. E. (1945). Fox squirrels and gray squirrels in Illinois. *Illinois Natural History Survey Bulletin* 23:449-536.
- Charter, M., Izhaki, I., Meyrom, K., Aviel, S., Leshem, Y., and Roulin, A. (2017). The relationship between weather and reproduction of the Barn Owl *Tyto alba* in a semi-arid agricultural landscape in Israel. *Avian Biology Research 10*:253-258.
- Choquenot, D. and Ruscoe, W. A. (2000). Mouse population eruptions in New Zealand forests: the role of population density and seedfall. *Journal of Animal Ecology 69* (6)*:*1058-1070.
- Climate & Weather Averages in Columbus, Ohio, USA. (2019). https://www.timeanddate.com/weather/usa/columbus/climate
- Costello, C. M., Jones, D. E., Inman, R. M., Inman, K. H., Thompson, B. C., and Quigley, H. B. (2003). Relationship of Variable Mast Production to American Black Bear Reproductive Parameters in New Mexico. *Ursus 14 :*1-16.
- Dantzer, B., Boutin, S., Humphries, M. M., and McAdam, A. G. (2012). Behavioral responses of territorial red squirrels to natural and experimental variation in population density. *Behavioral Ecology and Sociobiology 66* (6)*:*865-878.
- Dueser, R. D., and Shugart, H. H. (1978). Microhabitats in a forest-floor small mammal fauna. *Ecology 59* (1):89-98.
- Edelman, A. J., and Koprowski, J. (2006). Seasonal Changes in Home Ranges of Albert's Squirrels: Impact of Mating Season. *Canadian Journal of Zoology 84*:404-411.
- Flyger, V., and Gates, J. E. (1982a. Fox and gray squirrels. *Wild Mammals of North America*, ed. J. A. Chapman and G. A. Feldhamer, 209-229. Baltimore: Johns Hopkins University Press, 1147 p.
- Fox, J. F. (1981). Adaptation of Gray Squirrel Behavior to Autumn Germination of White Oak Acorns. *Evolution 36:*:800-809.
- Freeman, P. L. and Bachman, G. C. (2016). Disappearance and Mortality Causes in Thirteenlined Ground Squirrel (*Ictidomys tridecemlineatus*) Juveniles. *American Midland Naturalist 176* (1):130–146.
- Glass, G. E., and Slade, N. A. (1980). The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: Evidence for competition. *Ecology 62* (1):358-370.
- Goheen, J. R. and Swihart, R. K. (2003). Food-hoarding behavior of gray squirrels and North American red squirrels in the central hardwoods region: implications for forest regeneration. *Canadian Journal of Zoology 81:*1636-1639.
- Greenburg, C. H. and Zarnoch, S. J. (2018). A test of the predator satiation hypothesis, acorn predator size, and acorn preference. *Canadian Journal for Forest Research 48* (2)*:*237- 245.
- Gurnell, J. C. (1987). *The natural history of squirrels.* New York: Facts on File. New York City, NY.
- Hansen, L. P., and Nixon, C. M. (1986). Effects of adults on the demography of fox squirrels (*Sciurus niger*). *Canadian Journal of Zoology 63* (4):861-867.
- Hostetler, J. A., Kneip, E., Van Vuren, D. H., and Oli, M. K. (2012). Stochastic Population Dynamics of a Montane Ground-Dwelling Squirrel. *PLoS One 7* (3):1-10.
- Johnston, A. N., West, S. D, and Vander Haegen, W. M. (2019). Diets of Native and Introduced Tree Squirrels in Washington. *The Journal of Wildlife Management 83* (7): 1598-1606.
- Jokinen, M., Hanski, I., Numminen, E., Valkama, J., and Selonen, V. (2019). Promoting species protection with predictive modelling; Effects of habitat, predators and climate on the occurrence of the Siberian flying squirrel. *Biological Conservation 230:*37-46.
- Kamler, J. F., Ballard, W. B., and Wallace, M. C. (2007). Dietary Overlap of Swift Foxes and Coyotes in Northwestern Texas. *American Midland Naturalist 158*:139-146.
- Koprowski, J. L. (1991). Response of fox squirrels and gray squirrels to a late spring-early summer food shortage. *Journal of Mammalogy 72* (2):367-372.
- Koprowski, J. L. (1994a). *Sciurus carolinensis. Mammalian Species 480*:1-9.

Koprowski, J. L. (1994b). *Sciurus niger. Mammalian Species 479*:1-9.

- Kozlowski, A. J., Gese, E. M., and Arjo, W. M. (2008). Niche Overlap and Resource Partitioning Between Sympatric Kit Foxes and Coyotes in the Great Basin Desert in Western Utah. *American Midland Naturalist 160* (1):191-208.
- Lamontagne, J. M., Williams, C. T., Donald, J. T., Humphries, M. M., McAdam, A. G., and Boutin, S. (2013). Linking intraspecific variation in territory size, cone supply, and survival of North American red squirrels. *Journal of Mammalogy 94*:1048-1058.
- Leitner, B., and Leitner, P. (2017). Diet of the Mohave Ground Squirrel (*Xerospermophilus mohavensis*) in Relation to Season and Rainfall. *Western North American Naturalist 77* $(1):1-13.$
- Leon-Ortega, M., Mar Delgado, M. d., Martinez, J. E., Penteriani, V., and Calvo, J. F. (2016). Factors affecting survival in Mediterranean populations of the Eurasian eagle owl. *European Journal of Wildlife Research 62*:643–651.
- Lima, M., Morgan-Ernest, S. K., Brown, J. H., Belgrando A., and Stenseth, N. C. (2008). CHIHUAHUAN DESERT KANGAROO RATS: NONLINEAR EFFECTS OF POPULATION DYNAMICS, COMPETITION, AND RAINFALL. *Ecology 89*:2594–2603.
- Lima, S. L., Valone, T. J. and Caraco, T. (1985). Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Animal Behavior 33:*155-165.
- Ludwick, R. L., J. P. Fontenot, and H. S. Mosby. 1969. Energy metabolism of the eastern gray squirrel. *Journal of Wildlife Management* 33:569-575.
- Marolla, F., Aarvark, T., Oien, I. J., Mellard, J. P., Henden, J., Hamel, S., … Ims, R. A. (2019). Assessing the effect of predator control on an endangered goose population subjected to predator-mediated food web dynamics. *Journal of Applied Ecology 56* (5)*:*1245-1255.
- Mazzamuto, M. V., Bisi, F., Wauters, L. A., Preatoni, D. G., and Martinoli, A. (2017). Interspecific competition between alien Pallas' squirrels and Eurasian red squirrels reduces density of the native species. *Biological Invasions 19*:723–735.
- Moore, J. C. 1957. The natural history of the fox squirrel, *Sciurus niger shermani. Bulletin of the American Museum of Natural History* 113:1-71.
- Mosby, H. S. (1969). The influence of hunting on the population dynamics of a woodlot gray squirrel population. *Journal of Wildlife Management 33*:59-73.
- Neuhaus, P. (2000). Weight comparisons and litter size manipulation in Columbian ground squirrels (*Spermophilus columbianus*) show evidence of costs of reproduction. *Behavioral Ecology and Sociobiology 48* (1):75-83.
- Nixon, C. M., and McClain, M. W. (1969). Squirrel population decline following a late spring frost. *Journal of Wildlife Management 33*:353-357.
- O'Donoghue, M., Boutin, S., Krebs, C. J., and Hofer, E. J. (1997). Numerical Responses of Coyotes and Lynx to the Snowshoe Hare Cycle. *Oikos 80* (1):150-162.
- Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., and Reid, R. S. (2008). Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *Journal of Animal Ecology 77* (4):814–829.
- Parker, T. S., Gonzales, S., and Nilon, C. H. (2014). Seasonal Comparisons of Daily Activity Budgets of Gray Squirrels (*Sciurus carolinensis*) in Urban Areas. *Urban Ecosystems 17* (4)*:*969-978.
- Parker, T. S. and Nilon, C. H. (2008). Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosystems 11* (3)*:*243-255.
- Pokines, J. T., Santana, S. A., Heller, J. D., and Price, M. D. (2016). The Taphonomic Effects of Eastern Gray Squirrels (*Sciurus carolinensis*) Gnawing on Bone. *Journal of Forensic Identification 66* (4)*:*349-375.
- Prince, A., DePerno, C. S., Gardner, B., and Moorman, C. E. (2014). Survival and Home-Range Size of Southeastern Fox Squirrels in North Carolina. *Southeastern Naturalist 13* (3):456-462.
- Row, J. R., and Fedy, B. C. (2017). Spatial and temporal variation in the range‑wide cyclic dynamics of greater sage‑grouse. *Oecologia 185* (4):687–698.
- Schmidt, J. H., Rexstad, E. A., Roland, C. A., McIntyre, C. L., MacCluskie, M. C., and Flamme, M. J. (2018). Weather-driven change in primary productivity explains variation in the amplitude of two herbivore population cycles in a boreal system. *Oecologia 186* (2):435- 446.

Selonen, V., Wistbacka, R., and Korpimaki, E. (2016). Food abundance and weather modify

reproduction of two arboreal squirrel species. *Journal of Mammalogy 97* (5):1376- 1384.

- Selonen, V., Varjonen, R., and Korpimaki, E. (2014). Immediate or lagged responses of a red squirrel population to pulsed resources. *Oecologia 177* (1):401-411.
- Selonen, V. and Wistbacka, R. (2015). Siberian flying squirrels do not anticipate future resource abundance. *BMC Ecology 16* (1)*:*51-60.
- Sharpe, T. and Sherrill, B. (2017). Eastern Gray Squirrel. *Northern Carolina Wildlife Resources Commission*. https://www.ncpedia.org/wildlife/gray-squirrel

Smith, C. C., and Follmer, D. (1972). Food preferences of squirrels. *Ecology 53*:82-91.

- Spritzer, M. D. (2002). Diet, Microhabitat Use and Seasonal Activity Patterns of Gray Squirrel (Sciurus carolinensis) in Hammock and Upland Pine Forest. *American Midland Naturalist 148*: 271-281.
- Steele, M. A., and Koprowski, J. L. (2001). *North American Tree Squirrels.* Washington and London, Smithsonian Institution.
- Steele, M. A. and Smallwood, P. D. (1994). In press. Acorn dispersal by birds and mammals. In *Oak Forest Ecosystems: The Ecology and Management of Oaks for Wildlife*, ed. W. McShea and W. Healey. Baltimore: Johns Hopkins University Press.
- Steele, M. A., and Smallwood, P. D. (1994). What are squirrels hiding? *Natural History 103*:40- 45.
- The Ohio Wildlife Center. (2015). https://www.ohiowildlifecenter.org/
- Thompson, D. C. (1978). Regulation of a northern grey squirrel. *Behaviour 64*:305-328.
- Wallace, Z. P., Kennedy, P. L., Squires, J. R., Oakleaf, R. J., Olson, L. E., and Dugger, K. M. (2016). Re-Occupancy of Breeding Territories by Ferruginous Hawks in Wyoming: Relationships to Environmental and Anthropogenic Factors. *PLoS One 4*:1-16.
- Webley, G. E., and E. Johnson. 1982. Effect of ovariectomy on the course of gestation in the grey squirrel (*Sciurus carolinensis*). *Journal of Endocrinology* 89:107-116.
- "What is Mast?". (2009). *Mast Tree Network*. http://www.mast-producingtrees.org/2009/11/what-is-mast
- Vander Hagen, W. M. (2013). Survival and Causes of Mortality in a Northern Population of Western Gray Squirrels. *The Journal of Wildlife Management 77* (6)*:*1249- 1257.
- Xiao, Z., Gao, X., Jiang, M., and Zhang, Z. (2009). Behavioral adaptation of Pallas's squirrels to germination schedule and tannins in acorns. *Behavioral Ecology 20* (5):1050-1055.