FORAGING AND LIGHT AVOIDANCE THRESHOLDS IN WILD RODENTS EXPOSED TO DIFFERING LEVELS OF LIGHT POLLUTION

By

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FORAGING AND LIGHT AVOIDANCE

THRESHOLDS IN WILD RODENTS EXPOSED TO

DIFFERING LEVELS OF LIGHT POLLUTION

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Title of Study: FORAGING AND LIGHT AVOIDANCE THRESHOLDS IN WILD RODENTS EXPOSED TO DIFFERING LEVELS OF LIGHT POLLUTION

Major Field: ZOOLOGY

Abstract: I investigated whether light pollution alters foraging and light avoidance behavior in mice. I hypothesized that: 1.) exposure to light pollution would alter the natural shift in foraging behavior as illumination from the moon increases and 2.) light avoidance sensitivity is dependent on exposure to natural and artificial lighting in the environment. I conducted the study at four sites near Stillwater, Oklahoma that experience differing levels of light pollution. I measured nightly giving-up density in rodents from 16 foraging patches at each study site. I used linear regression models to find effects of light pollution on giving-up densities across a moon cycle. I used a Y-maze behavioral assay to estimate the mean light avoidance threshold in *Peromyscus leucopus* using the simple up-down method and compare them across all four sites using ANOVA. I found that mean GUDs grouped by light pollution level (low or high) when data were analyzed separately by year (2017: $F(1, 40) = 51.97$, $p < 0.001$; 2018: $F(1, 35) = 23.62$, $p < 0.001$; 2019: $F(1, 34) = 4.727$, $p = 0.04$) but not when all years were combined (All years combined: $F(1,114) = 0.265$, $p = 0.61$). Foraging activity responded to changing illumination from the moon only in 2017 at three sites (CCC - $F(1,9) = 14.71$, $p = 0.004$, BG - $F(1, 8) = 10.27$, $p = 0.01$ and IB - $F(1,9) = 19.44$, $p = 0.002$). The stimulus intensity for reversals in the Y-maze in males was significantly different among sites (ANOVA: $F(3, 31) = 11.09$, $p < 0.001$). Post-hoc Tukey analysis revealed stimulus intensity of male reversals was higher at the site with the greatest level of artificial light than at the other sites ($p < 0.02$ - 0.001). The stimulus intensities in which animals failed to respond to the light stimulus was independent of sex (Chi-squared: $X^2 = 7.24$, $p = 0.84$) and site (Chi-squared: $X^2 = 49.20$, $p = 0.07$) but dependent on reproductive status (Chi-squared: $X^2 = 69.12$, $p = 0.02$) for males (Chi-squared: $X^2 = 37.17$, $p = 0.01$) but not females (Chi-squared: $X^2 = 4.62$, $p = 0.87$).

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CHAPTER I

BACKGROUND

Falchi et al. (2016) mapped the distribution and magnitude of nighttime sky brightness, demonstrating that over 80% of the worldwide human population and 99% in the United States live where the nighttime sky is greater than 14 microcandelas per square meter ($\mu cd/m^2$) in brightness above natural background illumination; the level considered as light-polluted. This light pollution results from the increasing use of artificial lighting by modern human society (Falchi et al., 2016). Earth's atmosphere reflects this light and leads to a phenomenon called "sky glow," which in many areas can be equal to or greater than the magnitude of the full moon on a clear night: about 0.2 lux (Falchi et al., 2016; Longcore and Rich, 2004). This phenomenon blocks starlight and brightens the ambient nighttime environment over almost half of the land surface in the United States (Falchi et al., 2016). This may mask cues migrating animals use for navigation and interfere with the nocturnal ecology of the environment (Akesson et al., 2001; Longcore and Rich, 2004). Furthermore, vision in mammals transitions from being primarily cone mediated in bright conditions of daylight to rod mediated vision during the night. In many areas that experience high levels of light pollution this process of full visual dark adaptation (i.e., full scotopic vision) does not occur in humans

(Falchi et al., 2016).

LITERATURE REVIEW

LIGHT POLLUTION EFFECTS ON PHYSIOLOGY AND BEHAVIOR

Scientists increasingly recognize light pollution as a form of ecological contamination (Gaston et al., 2013; Longcore and Rich, 2004; Navara and Nelson, 2007; Riegel, 2001) because it may have several consequences to physiology and behavior in wild organisms (Bedrosian et al., 2013; Fonken et al., 2013; Gaston et al., 2013; Navara and Nelson, 2007). An early report documents possible effects due to increased light exposure to trees in New York City (Matzke, 1936). Matzke found trees along streets retained their leaves longer in the fall if they were in close proximity to street lights. Trees also retained leaves longer on the side facing the light while leaves dropped earlier on the side of the tree facing away from street lights (Matzke, 1936). In animals, alterations to orientation, reproduction, and other aspects of life history have been reported as possible outcomes of increased light exposure (Buchanan, 1993; Robert et al., 2015; Salmon, 2003; Salmon et al., 1995). These disturbances are thought to result from how animals use light for visual perception and orientation and how light affects their physiology (Gaston et al., 2013; Longcore and Rich, 2004).

Some effects of light pollution are due to its attractive quality for animals (Longcore and Rich, 2004; Salmon, 2003). For example, birds use light for nighttime migration (Poot et al., 2008) and are attracted to and often disorientated by point sources from boats, buildings, and other artificially lit human structures (Longcore and Rich, 2004; Poot et al., 2008). This can impact bird migration because of wasted energy costs during this critical period of their life history (Gauthreaux and Belser, 2006). Light

pollution also may disorient hatchling sea turtles resulting in higher mortality because it alters cues used in orienting toward the sea (Peters and Verhoeven, 1994; Salmon, 2003; Salmon et al., 1995).

Researchers also report behavioral changes to normal species interactions caused by light pollution (Longcore and Rich, 2004). Brighter skies extend the temporal occurrence of crepuscular lighting thereby allowing diurnal and crepuscular species to extend activity later into the evening or earlier into dawn (Longcore and Rich, 2004). Schwartz and Henderson (1991) found normally diurnal reptiles feeding underneath an outdoor light. Alteration to normal activity periods may disrupt temporal partitioning and increase competition between normally temporally separated species (Gutman and Dayan, 2005; Rotics et al., 2011). Prey species, such as moths, attracted to lights may be at greater risk of predation because of increased prey density in these areas (Frank, 1988; Rydell, 1992). Animals that feed on moths, such as bats, may in turn benefit from the increased prey density around these lights (Frank, 1988).

The light environment plays a big role in regulating normal behavior in animals (Borniger and Nelson, 2016; Jacob et al., 2017; Kotler et al., 2010). Physiologically, light is a major cue that entrains behaviors, hormonal secretion, and gene expression with daily and seasonal changes in photoperiod (Daan and Pittendridgh, 1976; Takahashi et al., 2008). These changes are necessary so that normal behaviors such as feeding and reproductive activities are conducted during the right time of day and season (DeCoursey et al., 2000; Takahashi et al., 2008). Increased light levels during nighttime may alter mechanisms maintaining the temporal consistency of these behaviors (Fonken et al., 2013; Fonken and Nelson, 2014). Implications may be wide ranging due to the

importance of these biological rhythms on overall physiological state (Fonken et al., 2013; Gaston et al., 2013).

BIOLOGICAL RHYTHMS

Biological rhythms are daily or seasonal fluctuations in gene expression and hormone profiles that control alternating states of metabolic activity and behavior such as sleep-wake cycles (Zelinski et al., 2014). These rhythms in mammals are manifestations of cyclically modulated gene complexes made up of circadian regulatory genes or "clock" genes active primarily within the suprachiasmatic nucleus (Reppert and Weaver, 2001). The suprachiasmatic nucleus (SCN), within the hypothalamus, controls these fluctuations via light information from photoreceptors in the eye, which then sets the phase or timing of these rhythms to match the light-dark cycle in a process called photoentrainment (Daan and Pittendridgh, 1976; Takashi et al., 2008; Zelinski et al., 2014). This process allows animal activity to closely follow daily changes in light level and photoperiod of any given 24-hour timespan (Zelinski et al., 2014). This biological rhythmicity is almost universally found in taxonomically diverse animals pointing to its adaptive importance (Rusak and Zucker, 1975; Zelinski et al., 2014). Disruptions to these circadian rhythms affect metabolic mechanisms (Zelinski et al., 2014) and activity patterns (Rojas-Castañeda et al., 2011) that impact animal survival and population persistence (DeCoursey et al., 2000).

Experiments in which animals were placed in enclosures with no outside information from the environment show that activity patterns are endogenous and have a period of about 24 hours (Pittendridgh and Daan, 1976; Rusak and Zucker, 1975).

However when external environmental stimuli are absent these activity patterns slowly become out of phase with those in animals that are receiving environmental information (Pittendridgh and Daan, 1976; Rusak and Zucker, 1975). These experiments point to the importance of light in regulating these behaviors and show the importance of the SCN in maintaining behavioral consistency through time (Daan and Pittendridgh, 1976).

The SCN is connected to the retina via a nerve tract running adjacent to the optic nerve called the retinohypothalamic tract (Takahashi et al., 2008; Zelinski et al., 2014). This nerve tract receives information from photoreceptors and transduces it to the SCN (Takahashi et al., 2008; Zelinski et al., 2014). Detection of light stimulates expression of clock genes within the SCN (Hannibal et al., 2001; Takahashi et al., 2008), resets the phase of biological rhythms, and allows gene expression and its consequent hormonal and behavioral cycles to closely follow changing external daily and seasonal cues (Takahashi et al., 2008).

Within the SCN, clock gene transcription is regulated by negative feedback (Takahashi et al., 2008). A good example is the PER1-CRY interaction with CLOCK-BMAL1. CLOCK and BMAL1 proteins act as transcription factors for the expression of *Per* and *Cry* regulatory genes. PER and CRY proteins chemically combine into dimers and interfere with CLOCK-BMAL1 proteins in the nucleus which inhibits transcription of *Per* and *Cry* genes. This process repeats itself about every 24 hours (Zelinski et al., 2014).

Recent research attempts to understand how increases in artificial nighttime lighting may affect behavior and gene expression in rodents (Bedrosian et al., 2013; Fonken et al., 2013; Jacob et al., 2017). Mice (*Mus musculus)* exposed to 5 lux dim light

at night in the lab, exhibited reduced activity (Bedrosian et al., 2013). Furthermore, expression of circadian clock genes *Bmal1*, *Per1*, *Per2*, *Cry1*, and *Cry2* were reduced in liver tissues and *Per1* and *Per2* expression was reduced in the hypothalamus along with their protein products (Fonken et al., 2013). Reduced gene expression may be explained by the nighttime light sensitivity of *Per1* and *Per2* (Matějů et al., 2009). Light inhibits expression of these genes at nighttime but not during the day (Matějů et al., 2009). More research must be conducted to determine if these same effects are found in wild populations and what selective pressures increase or decrease their sensitivity. Studying foraging behavior in wild animals under different lighting conditions may illuminate important factors that link altered behavioral mechanisms and light pollution.

FORAGING STUDIES

Researchers often study foraging behavior to gain understanding of environmental factors important for animal behavior. Ecologists have developed several models that predict foraging behavior in relation to energy costs (Brown, 1988; Charnov, 1976; Schoener, 1971). Optimal Foraging Theory states animal behavior reflects biological need to maximize energy input, and likewise fitness, while minimizing costs of obtaining that energy (Schoener, 1971). These costs include energy required to find and obtain resources and costs of failing due to predation. The optimal strategy does not always result in the maximum amount of energy obtainable but an overall higher yield after costs. This strategy mathematically results in higher overall reproductive fitness and greater number of genes passed to the next generation (Schoener, 1971). However, there are many factors to consider when predicting patterns of animal foraging behavior.

Research points to both biological and non-biological factors as covariates of behavioral outcomes (Wimer and Wimer, 1985). Non-biological factors include environmental conditions such as ambient temperature, weather, and lighting. Biological factors include physiological states such as hunger, body temperature, reproductive status, disease, parasite load, and gene expression (Sih et al., 2015; Wimer and Wimer, 1985). These factors may interact to produce the observed outcomes (Cid et al., 2015). For example, agoutis (*Dasyprocta azarae*) shift daily activity patterns during the hottest times of the year (Cid et al., 2015). Some researchers propose the costs of increased thermoregulation needed for foraging during these times is too high and agoutis benefit from reduced metabolic energy loss by shifting activity to reduce their energy demand (Cid et al., 2015).

Environmental dynamics also play a role in foraging behavior. Resources are usually not spread out homogeneously across a landscape but are clumped in patches that have higher energy density per unit area relative to the surrounding environment (Charnov, 1976). This clumping forces animals to allocate time in locating food. Since foraging animals are at increased risk of encountering a predator, researchers predict prey species should exhibit behavioral characteristics that minimize this risk (Schoener, 1971). These behaviors may manifest as preferences in microhabitat or temporal patterns that minimize the risk of predation for a given species. Once an animal locates a patch it begins harvesting its resources. But how long should the animal remain within the patch? There is a tradeoff between amount of food or energy an animal harvests over time and risk of predation by staying in a patch (Brown, 1988). The longer the animal remains the greater its probability of predation. Therefore a maximum amount of time spent within a

patch is predicted to optimize energy gained with risk of predation. An initial estimation of this time is predicted by the Marginal Value Theorem (Charnov, 1976).

The Marginal Value Theorem states a forager should remain on a patch as long as the net rate of energy gain is greater than the energy costs (Charnov, 1976). Therefore, it should leave the patch when the energy gained per unit time (e.g., the marginal value) becomes less than the average energy acquisition rate for the environment (Charnov, 1976). When an animal encounters a food-dense resource patch it initially harvests food items at a relatively fast rate. As the forager removes food the encounter rate decreases and the animal must spend an increasing amount of time and energy harvesting each subsequent item. Energetically, there are diminishing returns per unit energy harvested over time and the animal should leave when the rate of energy acquisition is no longer greater than it would be in the surrounding environment. This rate is known as the giving-up rate. However, since the instantaneous harvest rate for an individual is difficult to determine many researchers measure the giving-up rate indirectly through a related concept known as the giving-up density (GUD; Brown, 1988).

GUD is related directly to the giving-up rate because the density of food remaining over time in a patch determines the encounter rate and thus the giving-up rate (Brown, 1988). The technique gives a direct measurement of the willingness of animals to forage within a given food patch and is typically reported as the amount of food remaining in a food patch after a given amount of time (Brown, 1988). Animals are expected to minimize their risk of predation by spending less time foraging in patches with higher perceived risk, indicated by higher GUDs in those patches (Brown, 1988).

Scientists can then compare this measurement across different ecological situations to gain understanding about important factors for animal foraging behavior (Brown, 1988).

To measure GUD a researcher sets out artificial food patches with a known amount of bait mixed with substrate. The substrate is required to provide a more natural foraging experience. As an animal forages the density of food items within the substrate decreases and the animal must spend more time and energy finding each successive food item. GUD is simply the amount of food remaining in a patch over a given time (Brown, 1988). A higher GUD indicates animals spend less time foraging in a patch compared with a patch having a lower GUD. Because amount of time foraging is mediated by an animal's perceived risk of predation a researcher can use this method to identify preferences for habitat and temporal factors, such as lighting environment and weather, responsible for variation in foraging activity and predation risk (Brown, 1988). For example, Oyugi and Brown (2003) used GUD to learn that proximity to cover was important for determining where European Starlings (*Sturnus vulgaris*) and American Robins (*Turdus migratorius*) forage. GUDs were higher in habitat associated with danger and lower when patches were associated with canopy cover which presumably provides better cover from predators for these species (Oyugi and Brown, 2003).

Both gerbils (*Gerbilus andersoni*) and white-footed mice (*Peromyscus leucopus*) vary foraging effort with changing illumination from the moon (Jacob et al., 2017; Kotler et al., 2010). GUDs typically increase during the full moon indicating lower rodent activity during these times (Jacob et al., 2017; Kotler et al., 2010). This pattern may indicate an increase in perceived risk of predation during full moon due to the increased ability of their sight predators to locate prey in full moon conditions (Lima, 1998; Prugh

and Golden, 2014). Light pollution may also increase sight predator ability to capture prey. However, researchers investigating effects of light pollution on perceived risk of predation in rodents have reported mixed results based on rodent behavior (Bird et al., 2004; Persons and Eason, 2017). For example, beach mice (*Peromyscus polionotus*) forage less in artificially illuminated patches (Bird et al., 2004) but Persons and Eason (2017) found no effect of changing illumination of the moon on foraging behavior of *P. leucopus* in an urban environment in Kentucky. This is an interesting result because most research on foraging behavior in rodents, including this species, shows a clear reduction in activity during the full moon (Jacob et al., 2017; Kotler et al., 2010). The authors suggest light pollution may have altered normal responses of these mice to increased artificial illumination in this area (Persons and Eason, 2017). They suggest mice may have become habituated from longtime exposure to increased light levels or that light pollution does not produce the same behavioral responses as natural illumination (Persons and Eason, 2017). Wavelengths of artificial light pollution often differ from wavelengths from natural sources in the nighttime sky and may therefore affect animals differently from natural light (Gaston et al., 2013; Kyba et al., 2012). For example, LED lights emit photons across the spectrum but have peaks in the shorter wavelengths of blue and green (Kyba et al., 2012). This shift to shorter wavelengths may affect circadian rhythms of animals exposed because mechanisms responsible for maintaining circadian consistency are sensitive to blue light (Kyba et al., 2012; Rea et al., 2010).

Because artificial light increasingly encroaches on wildlife habitat it is important for researchers to continue investigating how increases in ambient environmental light affect animal behavior (Falchi et al., 2016; Longcore and Rich, 2004). Researchers must

consider the habitat and environmental conditions when making comparisons between studies. In studies of foraging behavior increased background illumination from light pollution may alter responses of animals and contribute to differences in results between studies. Physiologically, light pollution may alter sensitivity of animal responses to light stimuli by selecting for reduced sensitivity in gene expression or photoreceptor signal transduction in the retina (Akiyama et al., 2017; Prentice et al., 2017). This may manifest as reduced ability to behaviorally respond to light stimuli.

MEASURING RESPONSE SENSITIVITY

A common method of assessment for response sensitivity to psychophysical stimuli is the up-down or staircase method (Levitt, 1971; Klein, 2001; Wetherill and Levitt, 1965; Yokoi et al., 2014). The simple up-down method estimates a response threshold by providing a method that converges on the stimulus value giving a response from 50% of individuals subjected to a test stimulus (Levitt, 1971). The method requires sequential testing of one or more individuals to a test stimulus at a predetermined intensity. If the individual responds then the intensity of the test stimulus is reduced in the following trial (Levitt, 1971). This sequence continues until an individual fails to respond to the stimulus at which point the stimulus intensity is increased in the following trial. This is called a reversal. Trials continue until several reversals are obtained and the threshold is estimated by averaging the stimulus values at all the reversals in the sequence of trials (Levitt, 1971; Wetherill and Levitt, 1965). Results can be obtained after as few as 7 or 8 reversals have been recorded; however, García-Pérez (2000) recommends that at least 30 reversals be obtained for increased accuracy of the estimate. This method is

commonly used in psychoacoustics and vision research to estimate stimulus thresholds and contrast sensitivity and to investigate toxicological effects of chemical exposure (Gianfranceschi et al., 1999; Pelli and Bex, 2013; Prusky et al., 2000; Redfern et al., 2011; Wolski et al., 2003).

I was interested in how light pollution in the environment may affect rodent behavior. I explored two aspects of rodent behavior, foraging and light avoidance, important for understanding whether presence of light pollution plays a role. I measured GUDs across 4 sites with different levels of light pollution to investigate whether foraging varied with presence of increased environmental lighting. Because foraging is vital for survival I selected GUDs as the best method to investigate this phenomenon. If rodent foraging is affected by presence of light pollution their foraging response to changes in natural environmental illumination, i.e. from changing moon illumination, would be impacted because the light pollution could mask some of these natural changes. Furthermore, I was interested in how rodent light avoidance behavior is affected by presence of light pollution. If light avoidance is affected by increased ambient environmental light then rodents should behaviorally respond differently, based on site of capture, to a light source when placed within a Y-maze. I used a Y-maze to investigate whether wild *Peromyscus leucopus*, captured at study sites, show different sensitivities in behaviorally avoiding a lighted tunnel within the maze.

CHAPTER II

FORAGING IN WILD RODENTS UNDER DIFFERING LEVELS OF LIGHT POLLUTION

ABSTRACT

Anthropogenic consequences to natural environments are inevitable as the world becomes more populous; however, researchers can study these consequences to mitigate against possible negative outcomes. An increase in nighttime ambient light by means of artificial lighting has become a widespread issue with broad ranging impacts to animal behavior, populations, and broader ecosystems. Changes to animal foraging ecology may be affected by light pollution and potentially have broad implications for populations. I studied foraging by wild rodents at four different locations with differing levels of artificial light in and near Stillwater, Oklahoma (OSU Cross Country Course (CCC), OSU Botanic Garden (BG), Integrative Biology Field Ecology Land (IB), OSU Marshall Wheat Pasture Research Unit (MWP)) to better understand relationships between foraging ecology and light pollution. I measured nightly mean giving-up densities (GUDs) from foraging patches baited with whole black-oil sunflower seeds at all four sites over three years to find relationships between total foraging and whether animals respond similarly to changing moon illumination across sites. Mean GUDs grouped by light pollution level (low or high) when data were analyzed separately by year (2017:

$F(1, 40) = 51.97$, $p < 0.001$; 2018: $F(1, 35) = 23.62$, $p < 0.001$; 2019: $F(1, 34) = 4.727$, $p = 0.04$) but not when all years were combined (All years combined: $F(1,114) = 0.265$, $p = 0.61$). Foraging activity responded to changing illumination from the moon only in 2017 at three sites (CCC - $F(1,9) = 14.71$, $p = 0.004$, BG - $F(1, 8) = 10.27$, $p = 0.01$ and IB - $F(1,9) = 19.44$, $p = 0.002$).

Keywords – rodent, foraging, giving-up density, light pollution

INTRODUCTION

Falchi et al. (2016) mapped the distribution and magnitude of nighttime sky brightness, demonstrating that over 80% of the worldwide human population and 99% in the United States live where the nighttime sky is greater than 14 μcd/m^2 in brightness above natural background illumination; the level considered as light-polluted. This light pollution results from increasing use of artificial lighting in modern human society (Falchi et al., 2016). Earth's atmosphere reflects this light and leads to a phenomenon called "sky glow", which in many areas can be equal to or greater than the magnitude of the full moon on a clear night: about 0.2 lux (Falchi et al., 2016; Longcore and Rich, 2004). Vision in mammals transitions from being primarily cone mediated in bright conditions of daylight to rod mediated vision during night. In many areas that experience high levels of light pollution this process of full visual dark adaptation (i.e., full scotopic vision) does not occur in humans (Falchi et al., 2016). However, researchers do not know if light pollution affects visual dark adaptation in non-human animals. Sky glow blocks

starlight and brightens the ambient nighttime environment throughout almost half the land surface in the United States (Falchi et al., 2016). This may mask cues migrating animals use for navigation and interfere with the nocturnal ecology of the environment (Akesson et al., 2001; Longcore and Rich, 2004).

Scientists increasingly recognize light pollution as a form of ecological contamination (Gaston et al., 2013; Longcore and Rich, 2004; Navara and Nelson, 2007; Riegel, 2001) because it may have several consequences to physiology and behavior in wild animals (Bedrosian et al., 2013; Fonken et al., 2013; Gaston et al., 2013; Navara and Nelson, 2007). Alterations to orientation, reproduction, and other aspects of life history have been reported as possible outcomes of increased exposure to light (Buchanan, 1993; Robert et al., 2015; Salmon, 2003; Salmon et al., 1995). These disturbances result from how animals use light for visual perception and orientation and also how light affects their physiology (Gaston et al., 2013; Longcore and Rich, 2004).

Effects of light pollution are due in part to its attractive quality for animals (Longcore and Rich, 2004; Salmon, 2003). For example, birds use light for nighttime migration (Poot et al., 2008) and are attracted to and often disorientated by point sources from boats, buildings, and other artificially lit human structures (Longcore and Rich, 2004; Poot et al., 2008). This can impact bird migration because of wasted energy costs during this critical period of their life history (Gauthreaux and Belser, 2006). Light pollution also may disorient hatchling sea turtles resulting in higher mortality because it alters cues used in orienting toward the sea (Peters and Verhoeven, 1994; Salmon, 2003; Salmon et al., 1995).

Changes in behavior because of light pollution may also alter normal species interactions (Longcore and Rich, 2004). Brighter skies extend the temporal occurrence of crepuscular lighting. This allows diurnal and crepuscular species to extend their activity later into the evening or earlier into dawn (Longcore and Rich, 2004). Alteration to normal activity periods may disrupt temporal partitioning and increase competition between normally temporally separated species (Gutman and Dayan, 2005; Rotics et al., 2011). Prey species, such as moths, attracted to lights may attract more predators to an area and alter normal predator-prey interactions (Frank, 1988; Rydell, 1992). For example, Schwartz and Henderson (1991) found normally diurnal reptiles feeding underneath an outdoor light. Likewise, observers often report bats feeding on moths attracted by outdoor lighting (Frank, 1988).

The lighting environment plays a big role in regulating normal behavior in animals (Jacob et al., 2017; Kotler et al., 2010). Physiologically, light is a major cue that entrains behaviors, hormonal secretion, and gene expression with daily and seasonal changes in photoperiod (Daan and Pittendridgh, 1976; Takahashi et al., 2008). These changes are necessary so that normal behaviors such as feeding and reproductive activities are conducted during the right time of day and season (DeCoursey et al., 2000; Takahashi et al., 2008). Increased light levels during nighttime may alter mechanisms maintaining the temporal consistency of these behaviors (Fonken et al., 2013; Fonken and Nelson, 2014).

Experiments in which animals were placed in enclosures with no outside information from the environment show activity patterns are endogenous and have a period of about 24 hours (Pittendridgh and Daan, 1976; Rusak and Zucker, 1975).

However, because external environmental stimuli are absent these activity patterns slowly become out of phase with animals that receive environmental information (Pittendridgh and Daan, 1976; Rusak and Zucker, 1975). These experiments point to the importance of light in regulating these behaviors. Disruptions to circadian pathways affect metabolic mechanisms (Zelinski et al., 2014) and activity patterns (Rojas-Castañeda et al., 2011) that impact animal survival and population persistence (DeCoursey et al., 2000).

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GUD is related directly to the giving-up rate because the density of food remaining over time in a patch determines the encounter rate and thus the give-up rate (Brown, 1988). The technique gives a direct measurement of the willingness of animals to forage within a given food patch (Brown, 1988). Animals are expected to minimize

their risk of predation by spending less time foraging in patches with higher perceived risk, indicated by higher GUDs in those patches (Brown, 1988). Scientists can then compare this measurement across different ecological situations to gain understanding about important factors for animal foraging behavior (Brown, 1988).

To measure GUD a researcher sets out artificial food patches with a known amount of bait mixed with substrate. The substrate is required to provide for natural rodent foraging. As an animal forages the density of food items within the substrate decreases and the animal spends more time and energy finding each successive food item. GUD is simply the amount of food remaining in a patch over a given time (Brown, 1988). A higher GUD indicates animals spend less time foraging in a patch compared with a patch having a lower GUD. Because amount of time foraging is mediated by an animal's perceived risk of predation a researcher can use this method to identify preferences for habitat and temporal factors, such as lighting environment and weather, responsible for variation in foraging activity and predation risk (Brown, 1988). For example, Oyugi and Brown (2003) used GUD to learn that proximity to cover was important for determining where European Starlings (*Sturnus vulgaris*) and American Robins (*Turdus migratorius*) forage. GUDs were higher in habitat associated with danger and lower when patches were associated with canopy cover which presumably provides better cover from predators for these species (Oyugi and Brown, 2003).

Both gerbils (*Gerbilus andersoni*) and white-footed mice (*Peromyscus leucopus*) vary foraging effort with changing illumination from the moon (Jacob et al., 2017; Kotler et al., 2010). GUDs typically increase during the full moon indicating lower rodent activity during these times (Jacob et al., 2017; Kotler et al., 2010). This pattern may

indicate an increase in perceived risk of predation during full moon (Lima, 1998; Prugh and Golden, 2014). However, researchers have investigated effects of light pollution on perceived risk of predation in rodents with mixed results (Bird et al., 2004; Persons and Eason, 2017). For example, beach mice (*Peromyscus polionotus*) forage less in artificially illuminated patches (Bird et al., 2004). However, Persons and Eason (2017) found no effect of changing illumination of the moon on foraging behavior of *P. leucopus* in an urban environment in Kentucky. This is an interesting result because most research on foraging behavior in rodents, including this species, shows a clear reduction in activity during the full moon (Jacob et al., 2017; Kotler et al., 2010). The authors suggest light pollution may have altered normal responses of these mice to increased artificial illumination in this area (Persons and Eason, 2017). They suggest mice may have become habituated from longtime exposure to increased light levels or that light pollution does not produce the same behavioral responses as natural illumination (Persons and Eason, 2017). Wavelengths of artificial light pollution are often different from wavelengths of natural light in the nighttime sky (Gaston et al., 2013; Kyba et al., 2012).

Because artificial light increasingly encroaches on wildlife habitat it is important for researchers to continue investigating how increases in ambient environmental light affect animal behavior (Falchi et al., 2016; Longcore and Rich, 2004). Researchers must consider the habitat and environmental conditions when making comparisons between studies. Increased background illumination from light pollution may alter foraging behavior of mice and contribute to differences in results between studies.

I investigated foraging behavior of rodents in habitats under different levels of light pollution. Because presence of unnatural levels of light may increase risk of

predation in nocturnal species I predicted rodents would forage less in areas with more light pollution and hypothesized that effects of light pollution could be measured as differences in how rodents naturally adjusted foraging patterns with changing moon phases. I predicted in more light polluted areas rodents would not adjust foraging patterns during the darker new moon phases because of extra artificial lighting in the environment that may mask changes in sky brightest. A similar study found mixed results under light pollution levels nearly twice the magnitude as in this study (Persons and Eason, 2017). My work seeks to understand how relatively low levels of light pollution impact foraging behavior. All work was conducted under approved OSU IACUC ACUP AS-17-11.

METHODS

This study took place at 4 locations near Stillwater, Oklahoma. Locations included: 1) property managed by the OSU Marshall Wheat Pasture Research Unit (MWP) about 50.5 km west of Stillwater, in Logan County, OK; 2) OSU Department of Integrative Biology research land (IB) 16.7 km west of Stillwater; 3) OSU Botanic Garden (BG) 3.7 km west of Stillwater; 4) the OSU Cross Country Course (CCC) located just east of the Stillwater Regional Airport within Stillwater city limits. The last three sites are in Payne Co. OK. These four sites were chosen because they represent a gradient of light pollution based on data from Falchi et al. (2016; Fig 1.) and I expected them to have similar rodent communities based on presence of similar habitat and close geographic proximity to each other.

All four study sites are within the Cross Timbers ecoregion in north-central Oklahoma. Each site has a mixture of closed and open canopy as well as areas of no

canopy with most common tree species being Blackjack oak (*Quercus marilandica*) and Post oak (*Quercus stellata*) interspersed by prairie grasses. Eastern red cedar (*Juniperus virginiana*) is also present at all four sites but is more prevalent at CCC. Because percent canopy cover (% CC) and low vegetative cover (LVC) are important components of rodent habitat and affect amount of light illuminating foraging habitat I measured these characteristics at each site seasonally (Jacob et al., 2017). To measure % CC I took a series of vertical photographs at each site using a 12 megapixel camera on a Samsung Galaxy S8 smartphone. I placed the camera on a tripod 1 m above the ground. I took 16 photographs along a 4 x 4 grid with each photo being 10 m apart. Photographs were then processed using ImageJ image processing software (Schneider et al., 2012). Photos were converted to binary images and % CC of each photo was calculated by taking the percentage of pixels representing canopy vegetation. I recorded this measure as % CC for each foraging patch at a site. I used ANOVA to compare % CC among sites. I defined low vegetative cover (LVC) as percentage vegetation extending 0 - 0.5 m above the ground (Jacob et al., 2017). I determined LVC at each site seasonally using a 0.5 m x 1 m vegetation profile board similar to that used in previous studies but modified to measure only vegetation within 0.5 m of the ground (Jacob et al., 2017; Klein and Cameron, 2012). The board was marked with 100 light colored squares and 100 dark colored squares in a checkerboard pattern (Klein and Cameron, 2012). I took four readings of the board, one from each of the four cardinal directions, at each of the 16 grid stations per site. The same observer performed these readings throughout the study. For each reading a single photograph was taken at 1 m height and 3 m away from the board. From each photograph I counted the number of light colored squares in which ≥ 0.5 of the square is

visible (Jacob et al., 2017). Percent LVC for each reading is calculated as [((100 - # white squares visible)/100) * 100] (Jacob et al., 2017). I calculated %LVC for each station as the mean of the 4 readings at each station and compared mean %LVC for each grid yearly and all years combined. To compare %LVC between grid sites I used ANOVA.

At each study site I set out 16 artificial foraging patch stations placed 10 m apart in a 4 x 4 grid. Boxes were placed along edge habitat such that a portion of boxes were under closed or open canopy and a portion were placed under no canopy. In fall 2017 I used clear plastic containers that were ~ 4.9 L and had opaque lids. In 2018 and 2019 I used 5.7 L clear plastic containers (35.6 cm x 20.3 cm x 12.4 cm) having clear lids. I passed a nylon string through two holes drilled into the sides of each plastic container and staked them down with tent stakes. I also ran a nylon string over the top of each lid lengthwise and staked each end down. This prevented raccoons from tipping the container and spilling the contents. I also bolted down the lids of each container to prevent raccoons from removing the lid. Rodents entered a foraging patch through a 19 mm hole drilled into the end of the container. This hole size excluded larger species such as hispid cotton rats (*Sigmodon hispidus*) and eastern woodrats (*Neotoma floridana*) from entering containers. I baited stations with 6 g of black-oil sunflower seeds mixed into either 1 L of sand (2017) or 1.5 L of sand (2018 and 2019). The increase in sand volume in 2018 and 2019 was required to prevent GUDs going to 0. I set out baited stations three days prior to the start of each data collection phase for rodents to find and begin using the stations as food resource patches (Kotler and Brown, 1990).

Data collection took place simultaneously from all sites. This design allowed for direct comparison of rodent activity in relation to non-biological factors such as weather

and changes in moon illumination. I recorded mean temperature, mean humidity, and total 24 hour solar radiation data from the nearest Mesonet Weather Station (Brock et al., 1995; McPherson et al., 2007) to each site. Moon phase was recorded as the proportion of the moon illuminated at midnight of each night (USNO, 2017). A moon index was created by multiplying the proportion of the moon illuminated at midnight by the number of decimal hours the moon was above the horizon each night (Jacob et al., 2017).

Over the three year study period I collected foraging data across an entire moon cycle. In 2017 I collected data from 5 – 19 November. The proportion of the moon visible at midnight ranged from 0.98 – 0.01 (just after full moon to just after new moon). In 2018 I collected data from 5 – 24 May. The proportion of the moon visible at midnight ranged from 0.76 – 0.72 (approximately first quarter – third quarter phase). Based on data obtained from Oklahoma Mesonet (Brock et al., 1995; McPherson et al., 2007), flooding started on 20 May 2019 and lasted until early June in 2019. Due to this flooding the collection period took place in early May and mid-June in 2019. During May and June 2019 Stillwater received 54.63 cm of rain and Marshall received 65.43 cm of rain (Brock et al., 1995; McPherson et al., 2007). I collected data from 14 May – 17 May 2019, 12 June – 16 June 2019. The proportion of the moon visible at midnight from 14 May – 17 May 2019 was 0.74 – 0.97 (just before third quarter phase to just before full moon). The proportion of the moon visible at midnight from 12 June – 16 June 2019 was 0.72 – 0.99 (just before third quarter phase to just before full moon).

Stations were left overnight. Each day I sifted the sand at each station to separate sunflower seeds so they could be weighed using a Pesola scale. GUD was recorded as the mass (g) of sunflower seeds remaining in each station. I obtained 30 nights of data at

CCC, 30 nights at BG, 29 nights at IB, and 30 nights at MWP during the study for a total of 1818 patch-nights consisting of 461 (CCC), 445 (BG), 457 (IB), and 455 (MWP) total patch-nights at each site. This effort is comparable to previous studies investigating GUDs and activity of rodents in various habitats (Brown, 1988; Cid et al., 2015; Jacob et al., 2017). To understand species using sites I trapped rodents when the GUD patches were not active. During trapping I set out up to 192 Sherman® live traps baited with peanut butter and rolled oats. I analyzed similarity of rodent species captured by calculating the Dice Similarity Coefficient (DSC) between each site (Cheetham and Hazel, 1969).

I also calculated proportion of patches foraged for each night of the study at each site. Because raccoons frequently tipped over or broke into foraging boxes I needed to calculate the probability that a box would be foraged from had it been available throughout a given night. To do this I calculated the probability that a patch was foraged out of during a given year (the number of times a box was foraged from divided by the total number of nights of data collection each year). This probability was then added to the number of boxes foraged from and then divided by 16 to give the total patch-use on a given night for each site. I then compared mean log-GUDs with patch-use over the whole study and individual sites and years to investigate how patch-use affects GUDs using lm() in R.

I performed all statistical analyses using R (v 3.3.2—R Development Core Team 2013). If a patch had been turned over or otherwise tampered with by raccoons or other animals I did not record GUD for that patch for the given night. Because several GUDs reached 0 during 2017 and one patch reached 0 in 2019 I added 1 to each calculated GUD

during the study. I then base-10 log transformed each calculated GUD and obtained the mean log transformed GUD for each site consisting of all the GUDs obtained for each site for each night (Bowers et al., 1993; Mohr et al., 2003; Vickery et al., 2011). I defined CCC and BG as having high light pollution while IB and MWP were defined as having low light pollution. I tested for foraging differences between sites having high light pollution and low light pollution using ANOVA for all three years (2017, 2018, and 2019) combined as well as each year individually. I also tested for foraging differences during 2018 and 2019 combined. To test whether lid type may have affected GUDs I tested mean GUDs from 2017 against 2018/2019 combined mean GUDs using Welch Two Sample t-test. To analyze response to changing illumination from the moon I used linear regression for individual sites and years separately. Model design for individual sites was $Y = b0 + b1x_1$ where Y is the mean log-transformed giving-up density and x_1 is the illumination from the moon (moon index). I created models for each site individually for each year of the study (2017, 2018, and 2019) as well as a model using combined data from 2018 and 2019. I created individual yearly linear models for each site to analyze foraging response in relation to %LVC using the model design $Y = b0 + b1x1$ where Y is the mean log-transformed GUD and x1 is %LVC of each foraging patch. I also created a model analyzing combined data from 2018/2019. I also used the same model to analyze GUD response to %LVC for the combined sites having low light pollution and combined sites having high light pollution. Before using data for analysis any outliers were removed. Any data point less than 1.5 times the interquartile range (IQR) from the first quartile or more than 1.5 times the IQR from the third quartile was considered an outlier.

I compared mean daily temperature and total 24 hour solar radiation between sites using ANOVA.

RESULTS

Mean daily temperature ($F(3,1916) = 0.433$, $p = 0.73$) and total 24 hour solar radiation ($F(3, 115) = 0.329$, $p = 0.81$) were not significantly different among sites during the study; therefore, I did not include these variables in regression models. Overall mean %LVC at CCC, BG, IB and MWP (most to least light pollution) was 63.7, 61.5, 55.0, and 61.3, respectively. Mean %LVC was significantly different among sites ($F(3,1916) = 14.82$, $p < 0.001$). Post hoc TukeyHSD test revealed mean %LVC was significantly lower at IB compared to all other sites (CCC; $p < 0.001$, BG; $p < 0.001$, MWP; $p < 0.001$). Yearly mean %LVC for each site can be found in Table 1. Mean %CC at CCC, BG, IB and MWP for all three years was 35.5, 43.2, 51.4, and 32.1, respectively. Yearly %CC at each site can be found in Table 2. There were statistical differences in %CC between sites ($F(3,1916) = 32.9$, $p < 0.001$). Tukey test revealed %CC at CCC was less than BG ($p = 0.002$) and IB ($p = 0$). %CC at BG was less than %CC at IB ($p < 0.001$) and greater than %CC at MWP ($p < 0.001$). %CC was also significantly different between MWP and IB ($p < 0.001$).

I captured a total of 334 rodents of 6 species during the study over 10,570 trap-nights (Table 3). Total trapping effort for each site was 2,220 trap-nights at CCC, 2826 trap-nights at BG, 3,304 trap-nights at IB, and 2,220 trap-nights at MWP. Total numbers of rodents captured at each site were 72 (CCC), 94 (BG), 82 (IB), and 86 (MWP). Rodent communities at the four sites as indicated by species captured were similar. The DSC

between CCC and BG was 1, CCC and IB - 0.91, CCC and MWP - 1, BG and IB - 0.91, BG and MWP – 1, and IB and MWP - 0.91. Species common to all sites were *Peromyscus leucopus, Peromyscus maniculatus, Sigmodon hispidus, Neotoma floridana,* and *Reithrodontomys fulvescens*. The soricid species, *Blarina hylophaga,* was also captured at all sites except at CCC.

GUDs decreased as patch-use increased for all sites and all years combined ($F(1, 117) = 295.8$, $p < 0.001$; Fig. 2. GUD response to patch-use for individual sites and years can be found in Table 4. The combined sites having low light pollution (IB and MWP) showed responses in mean GUDs to increasing patch-use during 2017 ($F(1, 20) = 22.24$, $p < 0.001$), 2018 ($F(1, 16) = 22.22$, $p < 0.001$), 2019 ($F(1, 16) = 82.5$, $p < 0.001$), and 2018/2019 ($F(1, 35) = 119$, $p < 0.001$). The combined sites having high light pollution (CCC and BG) showed responses in mean GUDs to increasing patch-use during 2017 ($F(1, 18) = 54.89$, $p < 0.001$), 2018 ($F(1, 17) = 54.34$, $p < 0.001$), 2019 ($F(1, 16) = 23.45$, $p < 0.001$), and 2018/2019 ($F(1, 36) = 56.34$, $p < 0.001$).

Responses in GUD to changing %LVC for yearly models can be found in Table 5. I found a response in GUDs to increasing %LVC at the two combined sites having low light pollution (IB and MWP) only in 2017 ($F(1,335) = 19.72$, $p < 0.001$). At the two combined sites having high light pollution (CCC and BG) I found a significant response in GUDs to increasing %LVC during 2017 ($F(1,341) = 29.12$, $p < 0.001$), 2018 ($F(1,317) = 10.83$, $p = 0.001$), and 2018/2019 ($F(1,551) = 9.07$, $p = 0.003$).

Range of moon index was 0.01 – 12.33 in 2017, 0 – 5.11 in 2018, and 4.68 – 9.05 in 2019. The range of moon index for the combined 2018, 2019 data collection periods was 0 – 9.05. Mean log-transformed GUDs for the two sites having high light pollution

combined (CCC and BG, hereafter High Light Pollution) and the two sites having low light pollution combined (IB and MWP, hereafter Low Light Pollution) are shown in Fig. 3. Mean log-transformed GUDs for high light pollution sites and low light pollution sites combined for all three years were 0.703 ± 0.101 g and 0.691 ± 0.140 g, respectively. Mean log-transformed GUDs for individual sites are found in Table 6. There was no statistical difference in GUD between high light pollution and low light pollution during the three years combined ($F(1,114) = 0.265$, $p = 0.61$). Mean GUDs were significantly different in 2017 between High Light Pollution and Low Light Pollution ($F(1, 40) = 51.97$, $p < 0.001$). Post hoc TukeyHSD analysis showed that mean GUDs at Low Light Pollution sites were less than at High Light Pollution sites ($t = -7.06$, $p < 0.001$). Mean GUDs were significantly different in 2018 between High Light Pollution sites and Low Light Pollution sites ($F(1, 35) = 23.62$, $p < 0.001$). Post hoc TukeyHSD analysis showed that mean GUDs at Low Light Pollution sites were greater than at High Light Pollution sites ($t = 3.22$, $p < 0.001$). Mean GUDs were significantly different in 2019 between High Light Pollution and Low Light Pollution ($F(1, 34) = 4.727$, $p = 0.04$). Post hoc TukeyHSD analysis showed mean GUDs at Low Light Pollution were greater than at High Light Pollution ($p = 0.04$). Mean GUDs were significantly different in 2018/2019 between High Light Pollution and Low Light Pollution ($F(1, 70) = 26.28$, $p < 0.001$). Post hoc TukeyHSD analysis showed that mean GUDs at Low Light Pollution were greater than at High Light Pollution (Fig. 3; $p < 0.001$). Mean GUDs were significantly lower ($t(1, 68.51) = -3.21$, $p = 0.002$) in 2017 than in 2018/2019 combined. However, there was no difference in mean GUDs during the waxing phase of the moon during 2017, 2018, or 2019.

In 2017 there was a significant response to changing illumination from the moon at CCC ($F(1,9) = 14.71$, $p = 0.004$), BG ($F(1, 8) = 10.27$, $p = 0.01$) and IB ($F(1,9) = 19.44$, $p = 0.002$) (Fig. 4). In 2018 and 2019 there was no foraging response detected at any of the study sites; however, when data from 2018 and 2019 were combined there was a foraging response to changes in moon illumination at MWP ($F(1, 17) = 8.252$, $p = 0.01$) only.

DISCUSSION

Here I report that wild rodents forage differently where light pollution levels are elevated. Although I did not find support for my hypothesis that light pollution alters the magnitude of the foraging response I did find mean GUDs were different from areas with higher levels of light pollution compared to sites with lower levels of light pollution. Inconsistency in foraging response in this study may be due to other site specific characteristics, such as predator population, which affected the perception of risk across different years. This result is consistent with Persons and Eason (2017) who found that rodent foraging did not vary with moon illumination in an area that experienced nearly twice the magnitude of light pollution as in our study. In this study sites consistently grouped together by light pollution category although I report mixed results on the GUDs measured each season.

When I analyzed mean GUDs from all three years combined there was no difference in the mean amounts of seeds consumed across sites. This result is not surprising given that rodent populations may vary widely over time (Hayes et al., 2017; Wang et al., 2009) and disturbance can affect magnitude of rodent foraging (Bird et al.,

2004; Doherty et al., 2015; Jacob, 2003a). Therefore, combining foraging data from multiple years or seasons should be considered with caution. A thorough population study could better inform researchers on reasons for differences in rodent foraging between years. When I analyzed mean GUD data separately by year I obtained quite different results. Data from 2017 show rodents consumed significantly less from light polluted sites compared to sites with lower light pollution. This result is what I expected based on what is known about nocturnal rodent ecology (Persons and Eason, 2017). However, in 2018 and 2019 data show rodents consumed less on average from the two low light pollution sites. It is possible canopy cover may be masking effects of changing moon illumination. Mean %CC was lower in 2017 than in 2018 and 2019 at all sites probably due to seasonal variation in foliage. This would allow more light penetration and therefore may have altered the perceived risk of predation for mice. There may also have been human and animal disturbance at MWP and IB during 2018 and 2019. In April 2018 (about 4 weeks before data collection began) the grass at MWP was burned including where I set out foraging boxes. Mean %LVC was actually higher in 2018 at MWP probably because habitat data were collected 2 June which was a month and a half after the field was burned and grass had grown back. However, Conner et al., (2011) found lower survival rates of hispid cotton rats at recently burned study sites compared to control sites. They suggest prescribed fire alters habitat and increases risks from predation. Researchers have also observed lower vole population density after a flood (Jacob, 2003b). In 2019 cattle were being held on the pasture at MWP. There was also flooding during spring 2019 that affected timing of data collection at field sites. All or most boxes at BG and MWP were underwater during the flooding event. The other two

sites, CCC and IB, showed no sign of flooding. These events may have disrupted rodent foraging habitat and subsequently measured GUDs that year. Mean %LVC was much lower for BG and MWP in 2019 likely due to the flooding. Mean GUDs at MWP during 2018 and 2019 are indeed elevated over 2017 but not at BG. Mean GUDs at IB are also elevated over those of 2017. Although not quantified, I noticed a large tick infestation at IB during 2018 and 2019. High tick populations may affect the survival of rodents and thus population size which may affect GUDs (Hawlena et al., 2006) but results are mixed (Hersh et al., 2014). Lastly, the type of box lids used may have affected rodent foraging disproportionately at dark field sites. In 2017 I used opaque white lids that did not allow as much light to shine through while in 2018 and 2019 I used translucent lids. This difference may affect rodent foraging if rodents from darker reference sites are more sensitive to light. Rodents from lighter sites may be more tolerant of increased light while foraging because of the increased ambient light environment at night already present in light polluted areas.

In 2017 rodents decreased foraging as illumination from the moon increased at all sites except at MWP. They did not vary foraging in 2018 and 2019 at sites. However, when data from 2018 and 2019 were combined they did decrease their foraging at MWP as illumination from the moon increased but not at any of the other sites. These results highlight previous research reporting mixed results across studies (Farnworth et al., 2016; Kotler et al., 1993; Persons and Eason, 2017). In fact, Prugh and Golden (2014) found a wide range of responses to changing illumination from the moon across different rodent taxa. When studying wild populations researchers may encounter many factors that influence results. My data show all sites shared most of the same species and *P. leucopus*

was the most often captured species at each site. However, I did not conduct a population study to estimate population size of each species present at sites. Predominant species foraging from boxes may be different across sites and those species may have different responses to moon illumination and therefore influence results (Prugh and Golden, 2014). There may also be annual or seasonal differences in how wild rodents respond to light. Data in 2017 were collected in fall while data from 2018 and 2019 were collected in spring and early summer. Differences in overhead foliage may account for some variation in rodent foraging from particular boxes. Indeed mean %CC was lower for all sites in 2017 than in 2018 and 2019 with the exception of MWP, which had a lower mean %CC in 2019 than in 2017. Rodents may respond more strongly when boxes are placed under open or no canopy as opposed to a closed canopy (Prugh and Golden, 2014).

Researchers must also account for how much the moon changes during a study. In 2017 data covered the widest range of moon illuminations (0 – 12.33 moon index), while in 2018 and 2019 the moon index ranged from 0 to 5.11 and 4.68 to 9.05, respectively. In 2018 the short range in the change in illumination from the moon was due to the short timespans in which the moon was above the horizon during the night time. In 2019 the range was relatively small due to times in which data were collected. When analyzed individually the range of moon illumination may not have been sufficient to measure any foraging response using GUDs during 2018 and 2019. However, when I combined data from 2018 and 2019 the moon index ranged from 0 – 9.05 and rodents did respond at MWP but not at the other sites. The lack of response at the other sites may have been due to changes in conditions between years and/or vegetative cover. Again I recommend caution when combining data across years. For example, one factor influencing the

measured GUDs was patch use. Mean GUDs decreased as patch use increased. If patch use varies across years at a given site then combining mean GUDs across years could negatively affect model outcomes by masking time-sensitive responses and may be responsible for mixed results across years (Brown, 1999). However, I found that when sites were combined into low light pollution and high light pollution groups mean GUDs decreased as patch-use increased for all years.

Wild rodents also may be more sensitive to changes in illumination during a particular moon phase or season. Kotler et al., (2004) found GUDs were higher during the full moon and waning half-moon phase indicating moon phase is important in mediating rodent behavior. They suggest predator activity may increase during certain phases of the moon and affect rodent foraging during those times (Kotler et al., 2004). They also found GUDs were different between winter and summer months. I collected data in 2017 almost entirely during the waning phase of the moon, i.e. illumination from the moon was decreasing each day and in the fall. In 2018 I collected data 6 waning nights and 4 waxing nights in the spring. In 2019 I collected data in the spring and summer entirely during the waxing phase when illumination was increasing each day. Indeed mean GUDs were lower in 2017 and higher in 2018 at the Low Light Pollution sites relative to sites having high light pollution. However, there was no difference in mean GUDs during the waxing phase of the moon during 2017, 2018, or 2019.

Interestingly, rodents at sites with higher light pollution levels consistently foraged more from patches having higher %LVC than from patches with lower %LVC. This is consistent with findings by Jacob et al. (2017) and Persons and Eason (2017) regarding importance of LVC in rodent foraging decisions. However, low light pollution

sites did not show the same pattern. Only in 2017 did these sites show rodents foraging more in higher %LVC patches than in patches with lower %LVC. Light pollution may alter rodent decisions about what habitat is best for mediating risk of predation. In areas with low pollution foraging patches with lower %LVC may be perceived as less risky due to the darker skies relative to light polluted sites.

In conclusion, GUDs showed that wild rodents on average consumed different amounts of seeds from artificial foraging patches depending partially on whether populations are in habitat having low or high levels of light pollution; however, other environmental factors, such as disturbance, were also important. Sites consistently grouped together according to light environment supporting the hypothesis that light pollution can affect foraging in wild rodents. Rodents also varied foraging according to illumination from the moon during the first year of the study. This response was not consistent across years and sites indicating that local conditions and/or characteristics may play a more important role in influencing rodent foraging ecology than cyclical changes in ambient environmental light. Longer term studies and careful experimental design are needed to allow inferences regarding responses to different amounts of light pollution as well as what conditions are needed for rodents to vary their foraging according to moon cycle.

Table 1. The mean %LVC for each site during each year of the study. BG and MWP are lower during 2019 due to flooding at those sites.

	2017	2018	2019
CCC	51.7	64.4	70.8
BG	59.9	71.7	51.9
IB	44.0	62.3	60.3
MWP	64.1	70.7	47.3

Table 2. The yearly mean % Canopy Cover for each site.

	2017	2018	2019
CCC	22.2	36.5	50.7
BG	29.8	45.9	56.5
IB	43.2	54.3	58.3
MWP	29.8	40.9	25.3

Table 3. The total number of rodents captured at each site by year and the number of species captured. All rodent species were common to all sites except for *Mus musculus* which was only captured at IB.

	2017	2018	2019	2020	TOTAL	# Species
CCC	10	54	8	0	72	5
BG	12	48	13	21	94	5
IB	6	22	54	0	82	6
MWP	21	61	4	0	86	5
TOTAL	49	185	79	21	334	6

Table 4. The response in GUDs to increasing patch-use by site and year.

YEAR	SITE	VARIABLE	ESTIMATE	ST. ERROR	*t*-value	*p*-value
2017	CCC	intercept	0.936	0.033	28.674	3.72E-10
		patch-use	-0.487	0.059	-8.225	1.77E-05
	BG	intercept	0.843	0.011	79.182	7.21E-13
		patch-use	-0.13	0.038	-3.451	0.009
	IB	intercept	1.093	0.152	7.199	5.09E-05
		patch-use	-0.882	0.195	-4.528	1.00E-03
	MWP	intercept	0.875	0.053	16.498	4.92E-08
		patch-use	-0.414	0.07	-5.894	0.0002
2018	CCC	intercept	0.743	0.117	6.367	0.0004
		patch-use	-0.111	0.155	-0.719	0.496
	BG	intercept	0.855	0.010	89.48	2.72E-13
		patch-use	-0.282	0.023	-12.33	1.75E-06
	IB	intercept	0.843	0.013	65.79	4.93E-11
		patch-use	-0.239	0.066	-3.642	0.008
	MWP	intercept	0.850	0.004	219.2	1.08E-14
		patch-use	-0.141	0.019	-7.41	0.0001
2019	CCC	intercept	0.967	0.106	9.120	3.91E-05
		patch-use	-0.531	0.153	-3.471	0.010
	BG	intercept	0.687	0.025	27.49	1.04E-05

Table 4. Continued

YEAR	SITE	VARIABLE	ESTIMATE	ST. ERROR	*t*-value	*p*-value
		patch-use	0.009	0.069	0.133	0.901
	IB	intercept	0.842	0.029	28.77	1.17E-07
		patch-use	-0.360	0.124	-2.909	0.027
	MWP	intercept	0.909	0.034	27.10	2.39E-08
		patch-use	-0.497	0.072	-6.938	0.0002
2018/2019	CCC	intercept	0.846	0.102	8.324	2.12E-07
		patch-use	-0.310	0.139	-2.234	0.039
	BG	intercept	0.841	0.024	35.77	<2E-16
		patch-use	-0.294	0.057	-5.140	8.19E-05
	IB	intercept	0.855	0.014	62.50	<2E-16
		patch-use	-0.386	0.057	-6.791	4.34E-06
	MWP	intercept	0.881	0.018	49.92	<2E-16
		patch-use	-0.393	0.046	-8.454	1.71E-07

Table 5. The response in GUDs to increasing %LVC by site and year.

YEAR	SITE	VARIABLE	ESTIMATE	ST. ERROR	*t*-value	*p*-value
2017	CCC	intercept	0.676	0.043	15.58	<2E-16
		%LVC	-0.003	0.001	-4.441	1.22E-05
	BG	intercept	0.882	0.032	27.36	<2E-16
		%LVC	-0.001	0.001	-2.453	0.015
	IB	intercept	0.693	0.066	10.49	<2E-16
		%LVC	-0.006	0.001	-4.429	1.76E-05
	MWP	intercept	0.928	0.059	15.77	<2E-16
		%LVC	-0.006	0.001	-6.493	8.51E-10
2018	CCC	intercept	0.898	0.049	18.20	<2E-16
		%LVC	-0.004	0.001	-5.496	1.53E-07
	BG	intercept	0.813	0.047	17.34	<2E-16
		%LVC	-0.001	0.001	-1.13	0.260
	IB	intercept	0.882	0.038	23.50	<2E-16
		%LVC	-0.001	0.001	-2.130	0.035
	MWP	intercept	0.830	0.018	45.09	<2E-16
		%LVC	-0.0002	0.0002	-0.773	0.441
2019	CCC	intercept	0.450	0.092	4.895	3.02E-06
		%LVC	0.002	0.001	1.713	0.089
	BG	intercept	0.832	0.068	12.16	<2E-16

Table 5. Continued.

YEAR	SITE	VARIABLE	ESTIMATE	ST. ERROR	*t*-value	*p*-value
		%LVC	-0.003	0.001	-2.17	0.032
	IB	intercept	0.719	0.056	12.73	<2E-16
		%LVC	0.0004	0.001	0.430	0.668
	MWP	intercept	0.714	0.049	14.51	<2E-16
		%LVC	-0.0004	0.001	-0.425	0.671
2018/2019	CCC	intercept	0.754	0.047	16.03	<2E-16
		%LVC	-0.002	0.001	-2.882	0.004
	BG	intercept	0.760	0.038	20.135	<2E-16
		%LVC	-0.0004	0.001	-0.742	0.458
	IB	intercept	0.792	0.035	22.81	<2E-16
		%LVC	-0.0003	0.001	-0.493	0.623
	MWP	intercept	0.721	0.025	29.29	<2E-16
		%LVC	0.001	0.0004	1.93	0.06

Table 6. The mean log-transformed GUD (g) for each site during each year.

	2017	2018	2019	2018/2019
CCC	0.682 ± 0.095	0.660 ± 0.055	0.604 ± 0.081	0.622 ± 0.083
BG	0.811 ± 0.025	0.762 ± 0.079	0.691 ± 0.012	0.736 ± 0.080
IB	0.421 ± 0.180	0.806 ± 0.037	0.762 ± 0.039	0.776 ± 0.058
MWP	0.569 ± 0.078	0.829 ± 0.021	0.698 ± 0.110	0.760 ± 0.100

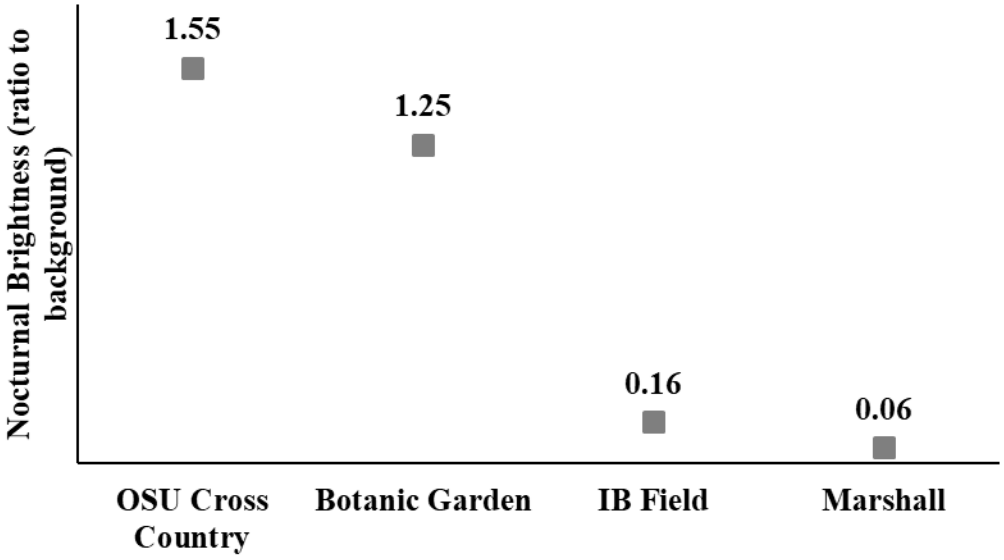

Figure 1. The brightness of the night sky (based on Falchi et al., 2016) at each of the study sites. Brightness decreases away from Stillwater, Oklahoma.

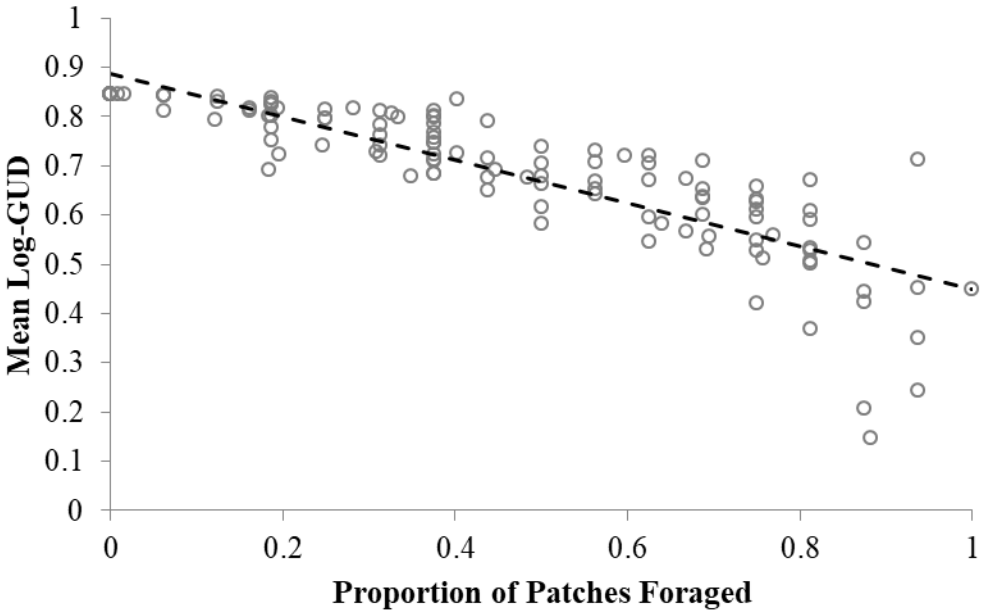

Figure 2. As patch-use increased across sites nightly mean GUDs decreased. $F(1,117) = 295.8$, Adjusted $R^2 = 0.71$, $p < 0.001$.

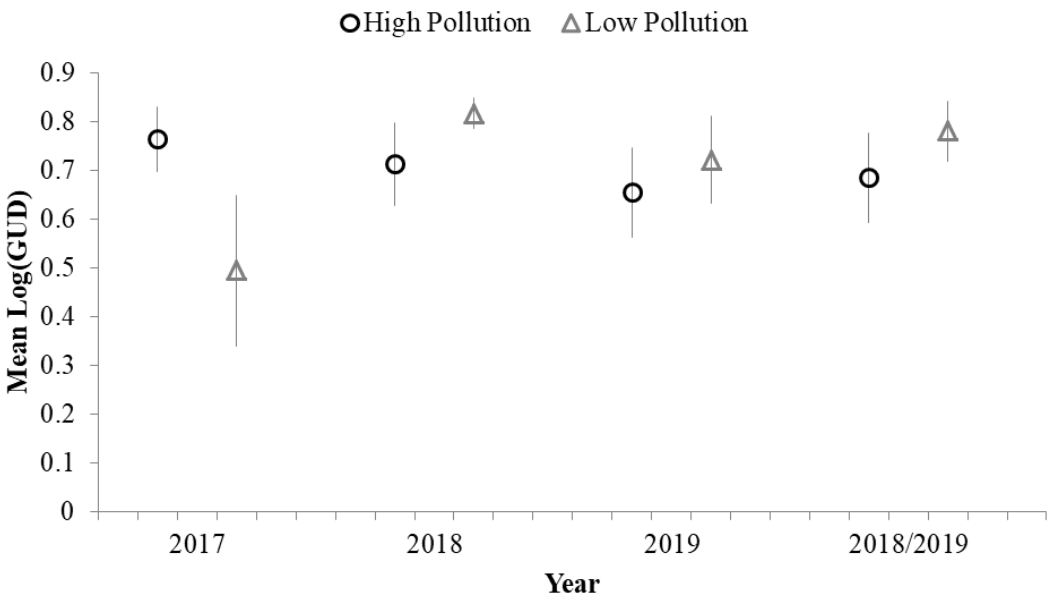

Figure 3. Mean log-transformed giving-up densities with standard deviations for combined sites having higher light pollution and those having low light pollution.

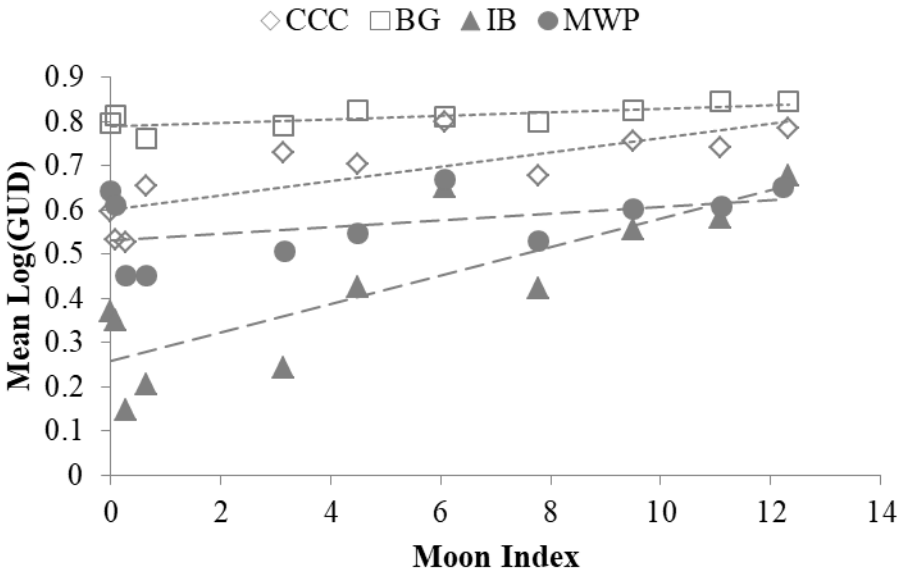

Figure 4. Foraging response at study sites in 2017. MWP was the only site to not exhibit a response to changing moon illumination.

CHAPTER III

BEHAVIORAL THRESHOLDS OF LIGHT AVOIDANCE IN *PEROMYSCUS LEUCOPUS* FROM ARTIFICIALLY LIT HABITATS

Abstract

With increasing urbanization light pollution has become prevalent throughout the world. This increased artificial light during the nighttime has the potential to disrupt animal behaviors ranging from migration, ecology, to reproduction. Because animals under light polluted skies may adapt to increased lighting I was interested in whether light avoidance behavior was altered in white-footed mice (*Peromyscus leucopus*). I captured mice from four study locations having a range of light pollution. I tested animals in a Y-maze behavioral assay in which animals were given a choice to go down an arm having an LED light turned on or one in which the light was off. Different animals were tested at different light intensities using the simple up-down method to calculate the mean light intensity at which animals failed to avoid the light (i.e. they went toward the light). The stimulus intensity for reversals in males was significantly different among sites (ANOVA: $F(3, 31) = 11.09$, $p < 0.001$). Post-hoc Tukey analysis revealed stimulus intensity of male reversals was higher in individuals from the site with the greatest level

of artificial light than at the other sites ($p < 0.02$ - 0.001). Stimulus intensity of male reversals was not different among the other three sites. The stimulus intensity of female reversals was not significantly different between the site with the least light pollution and the site with the second lowest level of light pollution (Welch t-test: $t = 0.5$, $p = 0.63$). The stimulus intensities in which animals failed to respond to the light stimulus was independent of sex (Chi-squared: $X^2 = 7.24$, $p = 0.84$) and site (Chi-squared: $X^2 = 49.20$, $p = 0.07$). The stimulus intensities in which animals failed to respond to the light stimulus was dependent on reproductive status (Chi-squared: $X^2 = 69.12$, $p = 0.02$). Further investigation showed stimulus intensities in which males failed to respond was dependent on their reproductive status ($X^2 = 37.17$, $p = 0.01$) but not for females (Chi-squared: $X^2 = 4.62$, $p = 0.87$).

Introduction

Falchi et al. (2016) showed that over 80% of the worldwide human population, including 99% in the United States, live where the nighttime sky is greater than 14 microcandelas per square meter ($\mu cd/m^2$) in brightness above natural background illumination; the level considered as light-polluted. This light pollution results from the increasing use of artificial lighting in modern human society. Earth's atmosphere reflects this artificial light and leads to a phenomenon called sky glow, which in many areas can be equal to or greater than the magnitude of the full moon on a clear night (Falchi et al., 2016; Longcore and Rich, 2004). Sky glow blocks starlight and brightens the ambient nighttime environment over almost half of the land surface in the United States (Falchi et al., 2016) which may mask cues migrating animals use for navigation and interfere with

the nocturnal ecology of the environment (Akesson et al., 2001; Longcore and Rich, 2004).

Scientists increasingly recognize light pollution as a form of ecological contamination (Gaston et al., 2013; Longcore and Rich, 2004; Navara and Nelson, 2007; Riegel, 2001) because it may have several consequences to physiology and behavior of wild animals (Bedrosian et al., 2013; Fonken et al., 2013; Gaston et al., 2013; Navara and Nelson, 2007). Vision in mammals transitions from being primarily cone mediated in bright conditions of daylight to rod mediated vision during the night. In many areas where there are high levels of light pollution this process of full visual dark adaptation (i.e., full scotopic vision) does not occur in humans (Falchi et al., 2016). In animals alterations to orientation, reproduction, and other aspects of life history have been reported as possible outcomes of increased light exposure (Buchanan, 1993; Robert et al., 2015; Salmon, 2003; Salmon et al., 1995). These disturbances result from how animals use light for visual perception and orientation and also how light affects their physiology (Gaston et al., 2013; Longcore and Rich, 2004).

Some effects of light pollution are due to its attractive quality for animals (Longcore and Rich, 2004; Salmon, 2003). For example, birds use light for nighttime migration (Poot et al., 2008) and are attracted to and often disorientated by point sources from boats, buildings, and other artificially lit human structures (Longcore and Rich, 2004; Poot et al., 2008). This can impact bird migration because of wasted energy costs during this critical period of their life history (Gauthreaux and Belser, 2006). Light pollution also may disorient hatchling sea turtles resulting in higher mortality because it alters cues used in orienting toward the sea (Peters and Verhoeven, 1994; Salmon, 2003;

Salmon et al., 1995). Researchers also report behavioral changes and alterations to normal species interactions caused by light pollution (Longcore and Rich, 2004). Brighter skies extend the temporal occurrence of crepuscular lighting which allows diurnal and crepuscular species to extend activity later into the evening or earlier into dawn (Longcore and Rich, 2004). Schwartz and Henderson (1991) found normally diurnal reptiles feeding underneath an outdoor light. Alteration to normal activity periods may disrupt temporal partitioning and increase competition between normally temporally separated species (Gutman and Dayan, 2005; Rotics et al., 2011).

The lighting environment plays a major role in regulating normal behavior in animals (Jacob et al., 2017; Kotler et al., 2010). Physiologically, light acts as a cue that entrains behaviors, hormonal secretion, and gene expression with daily and seasonal changes in photoperiod (Daan and Pittendridgh, 1976; Takahashi et al., 2008). These changes are necessary so normal behaviors such as feeding and reproductive activities are conducted during the right time of day and season (DeCoursey et al., 2000; Takahashi et al., 2008). Increased light levels during nighttime may alter mechanisms maintaining the temporal consistency of these behaviors (Fonken et al., 2013; Fonken and Nelson, 2014). Impact of light pollution may be wide ranging due to the importance of these biological rhythms on overall physiological state (Fonken et al., 2013; Gaston et al., 2013).

Recent research attempts to understand how increases in nighttime lighting may affect behavior and gene expression in rodents (Bedrosian et al., 2013; Fonken et al., 2013; Jacob et al., 2017). Mice (*Mus musculus)* exposed to 5 lux dim light at night in the lab, exhibited reduced activity (Bedrosian et al., 2013). Furthermore, expression of circadian "clock" genes *Bmal1*, *Per1*, *Per2*, *Cry1*, and *Cry2* were reduced in liver tissues

and *Per1* and *Per2* expression was reduced in the hypothalamus along with their protein products (Fonken et al., 2013). Reduced gene expression may be explained by the nighttime light sensitivity of *Per1* and *Per2* (Matějů et al., 2009). Light inhibits expression of these genes at nighttime but not during the day (Matějů et al., 2009). More research must be conducted to determine if modifications to these pathways are found in wild populations exposed to increased nighttime light levels and what selective pressures increase or decrease their sensitivity.

Researchers interested in effects of light pollution on perceived risk of predation in rodents have reported mixed results based on rodent behavior (Bird et al., 2004; Persons and Eason, 2017). For example, beach mice (*Peromyscus polionotus*) forage less in artificially illuminated patches (Bird et al., 2004) but Persons and Eason (2017) found no effect of changing illumination of the moon on foraging behavior of white-footed mice (*Peromyscus leucopus)* in an urban environment in Kentucky. This is an interesting result because most research on foraging behavior in rodents, including this species, shows a clear reduction in activity during the full moon (Jacob et al., 2017; Kotler et al., 2010). The authors suggest light pollution may have altered normal responses of these mice to increased artificial illumination in this area (Persons and Eason, 2017). They suggest mice may have become habituated from long term exposure to increased light levels or that light pollution does not produce the same behavioral responses as natural illumination (Persons and Eason, 2017). Studying light avoidance behavior in wild animals may illuminate important relationships between behavioral mechanisms and light pollution.

A common method of assessment for response sensitivity to psychophysical stimuli, such as light, is the up-down or staircase method (Levitt, 1971; Klein, 2001; Wetherill and Levitt, 1965; Yokoi et al., 2014). The simple up-down method estimates a response threshold by providing a method that converges on the stimulus value giving a response from 50% of individuals subjected to a test stimulus (Levitt, 1971). The method requires sequential testing of one or more individuals to a test stimulus at a predetermined intensity. If the individual responds then the intensity of the test stimulus is reduced in the following trial (Levitt, 1971). This sequence continues until an individual fails to respond to the stimulus at which point the stimulus intensity is increased in the following trial. This is called a reversal. Trials continue until several reversals are obtained and the threshold is estimated by averaging the stimulus values at all the reversals in the sequence of trials (Levitt, 1971; Wetherill and Levitt, 1965). Results can be obtained after as few as 7 or 8 reversals have been recorded; however, García-Pérez (2000) recommends that at least 30 reversals be obtained for increased accuracy of the estimate. This method is commonly used in psychoacoustics and vision research to estimate stimulus thresholds and contrast sensitivity and to investigate toxicological effects of chemical exposure (Gianfranceschi et al., 1999; Pelli and Bex, 2013; Prusky et al., 2000; Redfern et al., 2011; Wolski et al., 2003). Here I use the up-down method to determine if light pollution alters sensitivity of the light avoidance behavior in wild *P. leucopus*. Because of exposure to increased light levels at night I predicted animals in light polluted locations would be less sensitive to light than their dark site counterparts.

Materials and Methods

I live trapped wild *P. leucopus* at 4 locations near Stillwater, Oklahoma. Locations included: 1) property managed by the OSU Marshall Wheat Pasture Research Unit (MWP) about 50.5 km west of Stillwater, in Logan County, OK; 2) OSU Department of Integrative Biology research land (IB) 16.7 km west of Stillwater; 3) OSU Botanic Garden (BG) 3.7 km west of Stillwater; 4) the OSU Cross Country Course (CCC) located just east of the Stillwater Regional Airport within Stillwater city limits. Sites were chosen because they represent a gradient of light pollution. Using data from Falchi et al. (2016) I was able to determine the ratio of sky brightness relative to nighttime background illumination at CCC, BG, IB, and MWP is 1.55, 1.25, 0.16, and 0.06, respectively. I chose *P. leucopus* as the study species because of its documented nocturnal behavior (Baumgardner et al., 1980) and relative abundance in Oklahoma.

All four study sites are within the Cross Timbers ecoregion in north-central Oklahoma. Each site has a mixture of closed and open canopy as well as areas of no canopy. Because percent canopy cover (%CC) and low vegetative cover (%LVC) are important components of rodent habitat and affect amount of light illuminating foraging habitat I used data for these variables as described in Chapter 2 following methods of Jacob et al. (2017) to examine responses in the Y maze in relation to habitat.

I gathered data about the proportion of the moon illuminated at midnight from the U.S. Naval Observatory (USNO, 2017). I performed all statistical analysis using R (v 3.3.2—R Development Core Team, 2013). Trapping took place during spring, summer, and winter 2017 – 2020 during periods when the proportion of the moon illuminated was ≤ 0.5 to ensure animal trials were conducted under the same relative lighting. On each trapping night up to 192 Sherman live traps baited with rolled oats and peanut butter and

provisioned with cotton nesting material were set. Traps were opened shortly before sunset and left undisturbed overnight following standard trapping protocol (Sikes et al., 2016). Animals captured were transported in their trap to a windowless, metal field building at the IB site. Although the building was not completely free of incoming light I tested the light using a light meter (Sper Scientific, Scottsdale, Arizona) held at the point where trials were conducted (roughly the center of the building) and light intensity was below detectable limits (0.01 lux). Also the building was dark enough to elicit scotopic vision in the experimenter. I removed animals from traps by placing them in a cloth holding bag where they were identified, sex determined, and weighed (g) with a Pesola scale using the bag plus animal method. For males I categorized reproductive status as scrotal or nonscrotal. For females I categorized reproductive status as lactating or not lactating. I did not use pregnant females in analysis. I then left animals undisturbed for a minimum of 15 min before trials began. I performed all behavioral trials on the same morning each animal was captured. During times animals were in the building all lights were turned off. I used a headlamp with red light for illumination.

I conducted behavioral trials in a Y-maze apparatus constructed of 2 in (5.08 cm) diameter polyvinyl chloride (PVC) pipe. The entry tube where I introduced animals was 26.5 cm in length. At the point of choice, the maze splits into three separate tubes formed from a double-wye portion of PVC. The central opening is blocked by a GeekPro® sports camera modified to detect infrared light and mounted within a Styrofoam ball. Black electrical tape blocked any light emitted from the camera when turned on. To eliminate light emission from the view screen at the back of the camera a smartphone connected, via WiFi signal, to the camera turned the screen black upon connection and allowed

remote control of the camera. The smartphone screen displayed the camera view. I monitored animal movement within the maze via Wi-Fi connection between a smart phone app and the sports camera. The remaining two arms of the Y-maze are angled at 45 degrees relative to the entry tube and are 30 cm in length. Animals must change their direction of movement to go down one of these experimental arms. At the end of each experimental tube is a white LED light mounted inside the top of the PVC pipe and powered by two 3-volt batteries. Each white LED is connected to a potentiometer for control of light intensity. An infrared LED light illuminates the Y-maze at the point of choice. The ends of the Y-maze are capped so animals cannot fall or jump out of the maze.

I conducted behavioral trials according to the simple up-down method outlined in Levitt (1971) except for when trials were below 1 lux. For the purpose of this study, I defined a positive outcome as a trial in which an animal chose to go down the dark tube (i.e., it responded to the light stimulus by attempting to avoid it) and a negative trial outcome as one in which the animal chose to go down the lighted tube (i.e. it failed to respond to the light stimulus). I chose this method because the stimulus value behavioral trials converge on is the stimulus level in which 50% of trial outcomes are positive indicating random choice at which animals fail to respond to the light stimulus (Levitt, 1971). I was able to quantify the threshold stimulus value as the light intensity at which animals choose tubes randomly and therefore do not behaviorally distinguish between lighted versus dark tunnels.

I used only apparently healthy adult and subadult animals for behavioral trials. Males and females were statistically analyzed separately so that any sex differences in

light avoidance could be determined. Any animal that was an obvious recapture, indicated by distinct markings, was not rerun through the behavioral trial. Before each behavioral trial began I randomly chose the arm of the Y-maze in which the LED was turned on by toss of a die. I set the initial light intensity for the first trial in a series at 5 lux as measured by the light meter which corresponds with the predicted behavioral threshold light intensity for Sprague-Dawley rats (Wetherill and Levitt, 1965; Yokoi et al., 2014). Each animal completed only one behavioral trial. A trial began as soon as an animal was placed into the entry tunnel and ended after a two minute time period. During this time animals explored all tunnels of the maze and spread their scent throughout. This exploratory behavior of animals eliminated the need to clean the maze between trials to remove scent and avoid bias because scent from a previous animal was throughout the maze thus eliminating olfactory stimulus subsequent animals could use as a cue that could bias choice data (Lester, 1968). I defined the choice of the animal as the first tube the animal investigates such that its entire body, excluding tail, was completely in the tube. If this choice was to go down the dark tunnel (i.e., a positive outcome), in the next trial with a different animal, the light intensity was lowered by 2 lux. Positive outcomes below 1 lux resulted in lowering of light intensity of the subsequent trial by 0.5. If I obtained a positive outcome at 0.01 lux (the lowest measurable intensity) I recorded a 0 for the next trial and the subsequent trial was set at 1 lux. This sequence of trials continued until an animal chose to go down the lighted tube of the Y-maze (i.e., a negative outcome). At this point the light intensity was increased by 2 lux if the reversal occurred at or above 1 lux and was increased to 1 lux if the reversal occurred below 1 lux. This point was called a reversal because an animal chose to go down the tube with

the opposite stimulus than the previous animal. This sequence of trials continued until there were 7-8 reversals for each site. The threshold value was then calculated by taking the average of all the stimulus values of each reversal (Levitt, 1971). I performed ANOVA and Welch t-test in R to detect whether threshold levels were different among sites. I also checked whether animals were avoiding the light by performing a binomial test (binom.test) in R on behavioral trials conducted in which the stimulus lux was ≥ 1 lux. I checked to see if stimulus intensity at which animals failed to respond to the light stimulus was independent of sex, reproductive status, and site using a chi-squared (chisq.test) test in R. All work was conducted under approved OSU IACUC ACUP AS-17-11.

Results

Overall mean %CC at CCC, BG, IB and MWP was 35.5, 43.2, 51.4, and 32.1, respectively. There were statistical differences in % CC between sites ($F(3,1916) = 32.9$, $p < 0.001$). Tukey test revealed %CC at CCC was less than BG ($p = 0.002$) and IB ($p = 0$). %CC at BG was less than % CC at IB ($p < 0.001$) and greater than % CC at MWP ($p < 0.001$). % CC was also significantly different between MWP and IB ($p < 0.001$).

At CCC, BG, IB, and MWP I trapped for 2220, 2826, 3304, and 2220 trap-nights, respectively, and captured 170 *P. leucopus* (98 males, 72 females). I performed 144 behavioral trials (CCC: 21, BG: 42, IB: 41, MWP: 40) and 95 trials in which the stimulus intensity was ≥ 1 lux (Fig. 5). Under these conditions 67 animals chose to go down the dark tube. The probability that animals chose the dark arm when stimulus lux was ≥ 1 lux was not equal to 0.5 (Binomial test: $p < 0.001$) showing animals avoided the lighted

tunnel at or above this intensity level. The number of *P. leucopus* captured at each site and the number of reversals obtained can be found in Table 7. Because I did not reach the recommended number of reversals needed for statistical analysis for female animals at CCC and IB I report statistical data for females only from BG and MWP. I ran behavior trials on a total of 88 males (CCC:17, BG:25, IB:27, MWP:19) and 56 females (CCC:4, BG:17, IB:14, MWP:21). I captured a total of 9 scrotal males, 79 non-scrotal males, 15 lactating females, and 43 non-lactating females.

The mean stimulus intensity of male reversals at each site was: MWP--2.55 ± 2.46 lux; IB--0.83 ± 0.86 lux; BG--0.83 ± 1.04 lux; and CCC--5.8 ± 3.16 lux. The mean stimulus intensity of female reversals at each site was: MWP--2.06 ± 1.93 lux; BG--1.54 ± 1.82 lux. The stimulus intensity of male reversals was significantly different among sites (ANOVA: $F(3, 31) = 11.09$, $p < 0.001$). Post-hoc Tukey analysis revealed stimulus intensity of male reversals was higher at CCC than at BG ($p < 0.001$), IB ($p < 0.001$), and MWP ($p = 0.02$). Stimulus intensity of male reversals was not different among the other three sites. The stimulus intensity of female reversals was not significantly different between MWP and BG (Welch t-test: $t = 0.5$, $p = 0.63$). The stimulus intensities in which animals failed to respond to the light stimulus was independent of sex (Chi-squared: $X^2 = 7.24$, $p = 0.84$) and site (Chi-squared: $X^2 = 49.20$, $p = 0.07$). The stimulus intensities in which animals failed to respond to the light stimulus was dependent on reproductive status (Chi-squared: $X^2 = 69.12$, $p = 0.02$). Further investigation showed stimulus intensities in which males failed to respond was dependent on their reproductive status ($X^2 = 37.17$, $p = 0.01$) but not for females (Chi-squared: $X^2 = 4.62$, $p = 0.87$). The mean stimulus intensity at which non-scrotal males failed to respond was 2.39 ± 2.57 lux. The

mean stimulus intensity at which scrotal males failed to respond was 0.35 ± 0.45 lux. The stimulus intensity at which non-scrotal males failed to respond was significantly higher than the stimulus intensity at which scrotal males failed to respond across all sites (Welch t-test: $t = 3.39$, $p = 0.003$).

Discussion/Conclusion

Here I report a possible shift in the threshold of light avoidance behavior in wild male *P. leucopus* from a light polluted location compared to males at other sites. Female sensitivity at BG and MWP did not differ from the males at those sites. The light intensity at which mice randomly avoided the lighted tunnel in a Y-maze assay was much greater at the most light polluted site (CCC) compared to all other locations. This may be due to several factors related to the environment. Animals at this location may be more accustomed to life under light polluted skies and therefore brighter ambiant conditions. If they have greater tolerance for presence of light, I would expect that in a Y-maze assay this would be demonstrated as requiring a greater intensity of light stimulus to elicit avoidance behavior.

The light levels I tested mice under were comparable to laboratory studies and natural conditions in the field (Yokoi, 2014). Yokoi (2014) found the threshold for Sprague-Dawley rats was around 5 lux. But since light levels are much lower in the field I expected a lower threshold for wild mice (Falchi et al., 2016). The most light polluted site had a threshold greater than 5 lux for male mice, but lower thresholds occurred at the less polluted sites.

The mechanism for an increased tolerance may be genetic. Physiologically light pollution may alter sensitivity of animal responses to light stimuli by selecting for reduced sensitivity in gene expression or photoreceptor signal transduction in the retina (Akiyama et al., 2017; Prentice et al., 2017). This may manifest as reduced ability to behaviorally respond to light stimuli. Keene et al. (2011) found clear evidence of genetic control of light avoidance in *Drosophila*. Transcription of these genetic factors may shift in sensitivity and therefore alter retinal responsiveness leading to altered light avoidance behavior in some populations. Research also points to several signaling pathways in the optic system important for mediating behaviors (Baik et al., 2018; Johnson et al., 2010; Keene et al., 2011; Whipshaw, 1974).

I did not find a decrease in sensitivity in light avoidance at BG, the second most light polluted location. Although the light pollution difference is small ($\Delta 4.2$ $\mu cd/m^2$) the level at CCC may be enough that animals respond differently when placed in the behavioral assay. Light pollution at BG may simply not be intense enough to elicit a change in response as indicated by the response similarity to the two darker locations.

Another possible reason CCC differs from all other sites is the general land use in and around the study site (Jacob et al., 2017; Linzey et al., 2012; Persons and Eason, 2017). The CCC site is within Stillwater and adjacent to the airport. Furthermore, it is located within a more urban area compared to the other three sites and, therefore, is subject to other types of human disturbance that may affect sensitivity. However, I was not able to investigate these other possible variables. Further research investigating these variables could shed light on possible interactions between other forms of human disturbance and light pollution.

Foraging studies have found some discrepancies between rodent behaviors in urban versus rural locations (Jacob et al., 2017; Persons and Eason, 2017). Persons and Eason (2017) found that in rodents in an urban area having light pollution nearly twice as much as my study, increasing illumination from the moon did not correspond to changes in foraging behavior. The authors suggest light pollution may mask the natural changes in moon light and affect the typical decrease in foraging as illumination from the moon increases (Person and Eason, 2017). This behavioral change in a light polluted habitat may manifest as a decrease in the light avoidance behavior in rodents living in these locations and may be responsible for my results.

Since there were differences in habitat between some sites there remains the possibility that responses in the Y-maze were dependent on habitat characteristics found at those sites. Results for %CC are particularly interesting. The sites with the lowest mean %CC (CCC and MWP) had the highest light avoidance threshold. Of those two sites the one with the highest intensity of light pollution (CCC) also had the higher light avoidance threshold. The second most light polluted site (BG) also had the second highest %CC. Y-maze data and canopy cover data taken together suggest that higher amounts of canopy cover may partially mediate the light avoidance behavior and that light pollution at a site may decrease the sensitivity to light in *P. leucopus*. If low canopy cover is perceived by mice as having a higher risk of predation then areas having lower canopy cover may be perceived as more stressful. Ossenkopp et al. (2005) found that mice under stressful conditions increase their exploratory behavior. This finding may explain the decrease in sensitivity to light in this experiment at the location having the

lowest %CC. Further hormonal and behavioral research could shed light on possible correlations between canopy cover, light pollution, and light avoidance behavior.

There may also be a relationship between reproductive status and light avoidance. Gray (1978) found estrous female CD-1 mice were less fearful in a lighted compartment than non-estrous females. Also Avigdor et al. (2005) found secretion of gonadotropin-releasing hormone was related to the light-dark cycle in wild stock *P. leucopus*. This is interesting given my counterintuitive result that scrotal males failed to respond at significantly lower light intensity than non-scrotal males. This result may be due to possible hormonal differences related to a scrotal state. Scrotal animals may be more sensitive to light stimuli than non-scrotal males. However, more research needs to be completed to better understand this possibility.

In conclusion, I found partial support for the hypothesis that light pollution alters the sensitivity of light avoidance behavior in *P. leucopus*. Male mice at the most light polluted location were significantly less sensitive to light than at the other three sites. The sensitivity of the light avoidance behavior also appears to be mediated by the mean percentage of canopy cover at a given site. I found that the two sites with the least canopy cover had the lowest sensitivities although MWP was not significantly different from the other two sites (IB and BG). This result was due to the high degree of variability in sensitivity at this site which may indicate variability in the avoidance phenotype. More investigation into the light avoidance behavior and light pollution could help reseachers better understand behavioral sensitivity under light polluted conditions.

Table 7. The number of male and female *P. leucopus* captured at each site and the number of reversals obtained for each.

	CAPTURED			REVERSALS	
	MALE	FEMALE	TOTAL	MALE	FEMALE
CCC	21	8	29	10	2
BG	27	25	52	7	6
IB	28	15	43	10	3
MWP	22	24	46	8	7
TOTAL	98	72	170	35	18

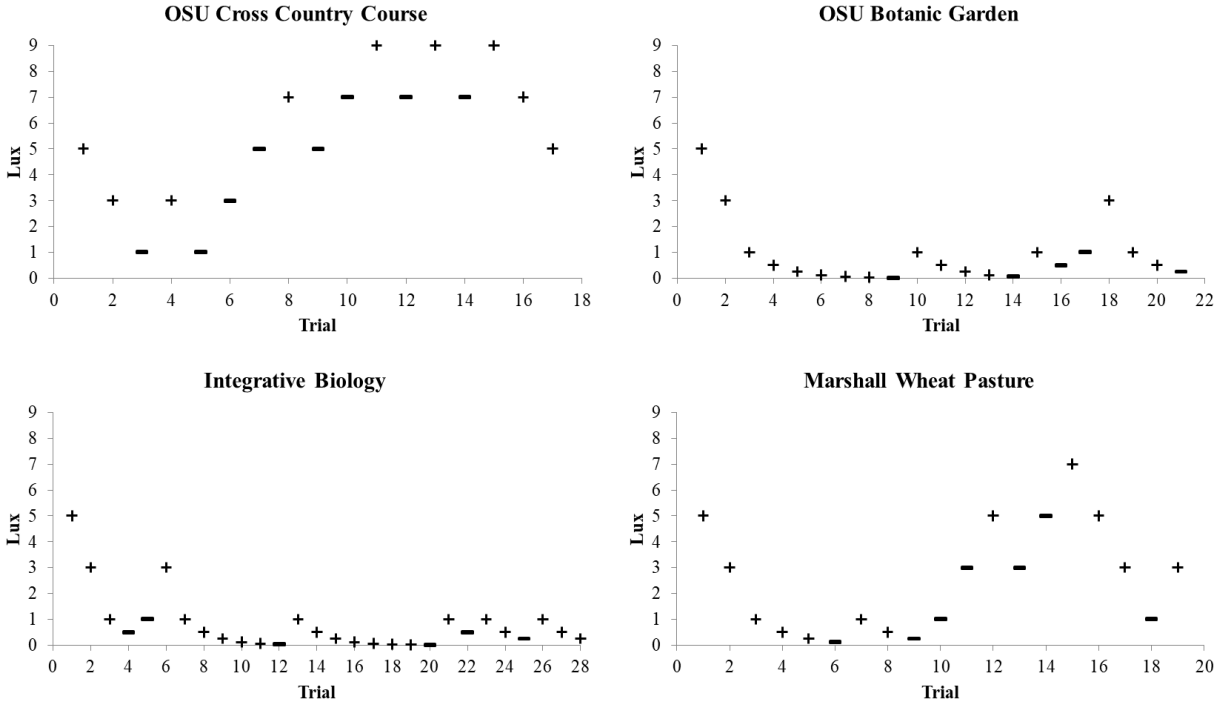

Figure 5. The up-down response sequence for all four study locations. (+) indicates animals responded to light stimulus. (-) indicates animals did not respond to light stimulus.

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