

ABSTRACT

BURGESS, MURRY L. The Role of Natural and Artificial Photoperiod on Songbird Physiology, Development, and Life History. (Under the direction of Dr. Caren Cooper).

Most organisms synchronize life history events with natural photoperiod, of which birds provide a great case study. In a changing environment that includes the rapid growth of artificial light at night (ALAN), it is imperative to understand the mechanisms and feedback loops by which photic input is received and interpreted, and how ALAN might interrupt those systems. In Chapter 1, I use a large citizen science database to model how natural photoperiod shapes the clutch size of Eastern Bluebirds. I found that daily changes in photoperiod are the strongest predictor of Eastern Bluebird clutch size patterns. In Chapter 2, I conduct a field experiment with Barn Swallow nestlings to see how they develop morphology and physiology under ALAN. I found that nestlings develop morphology slower and tail feathers faster in ALAN, although ALAN had no impact on physiological measurements or body condition, or brood success. Finally in Chapter 3, I synthesize case studies on skyglow and its impact on ecology, as well as explore potential solutions to mitigate negative physiological effects on birds.

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The Role of Natural and Artificial Photoperiod on Songbird Physiology and Development

by
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DEDICATION

I dedicate this dissertation to my family.

To my parents, who in every way encourage and support my love for animals, writing, and learning. To my grandparents, who pray and proudly watch on (from a safe distance from the wildlife). To my great-grandfather, who sowed the seeds for generations to bloom. To a host of uncles, aunts, and cousins who continuously cheer me on. To my closest friends, who are family too, and put a smile on my face when I most need it. And to Loki, the best emotional support gremlin in the world.

BIOGRAPHY

Murry Louida Burgess grew up in the suburbs of Minnesota, Florida, Tennessee, and Mississippi with an interest in the wildlife around her. She followed this interest into a degree in Wildlife, Fisheries, and Aquaculture at Mississippi State University, earning her B.S. in 2019. She also earned her Associate Wildlife Biologist® certification from The Wildlife Society. Murry went on to graduate school at North Carolina State University to pursue a Ph.D. in Fisheries, Wildlife, and Conservation Biology. She joined Dr. Caren Cooper's Public Science Lab where she studied urban ecology and ornithology, with a focus on the effects of anthropogenic stressors on songbird health and development. Murry's next step is moving into a tenure-track Assistant Professor position in the Wildlife, Fisheries, and Aquaculture Department at Mississippi State University.

Murry's work extends past wildlife and ecology research. While in Dr. Cooper's lab, Murry also found her passion for science communication and diversity, equity, and inclusion (DEI) advocacy. In 2022, Murry co-founded Field Inclusive, a nonprofit dedicated to amplifying and supporting marginalized field researchers in the natural sciences through providing financial aid and field safety resources. Her and her nonprofit's work have been highlighted in several publications, including *Audubon*, *Discover Magazine*, *Spectrum News*, and *Backyard Ecology Podcast*. In addition, Murry is a children's author with both self-published work and a contract with Little, Brown Young Readers and Christy Ottaviano Books for a nature books series featuring a 5-year-old Black girl exploring the nature around her suburban home. Murry plans to continue to combine ecology, DEI, and storytelling in her future work and career.

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CHAPTER 1: Change in Photoperiod Best Describes Pattern of Clutch Size in Eastern Bluebirds

I. Introduction

A predominant ecological trend that has been recognized for about a century is that clutch size follows a latitudinal gradient. Avian clutch size increases from the equator towards the poles both within and across species (Moreau 1944; Lack 1947), especially in passerines. Extensive thought about clutch size has produced several explanations for latitudinal patterns, such as daylength, seasonality, predation, or physiology. An equally ubiquitous pattern is seasonal decline in clutch size relative to lay date (Hochachka 1990; Goodenough et al. 2009). In a rapidly changing environment, it is important to nail down the mechanism(s) determining clutch size and how they might be affected by anthropogenic stressors. Although this paper focuses on birds, many taxa follow similar latitudinal patterns.

A. Variation Across Latitude

Lack (1947) hypothesized that clutch sizes are larger in the north because longer daylengths allow for more time to gather resources during the breeding season. Lack's hypothesis assumes that clutch sizes are limited by the subsequent amount of food parents will be able to bring to nestlings (Lack 1947; Royama 1969; Rose & Lyon 2013). Lack was vague about the physiological mechanisms by which daylength could influence clutch size, but generally implied a relationship between resource availability and parental feeding of chicks. Although, some empirical studies have failed to find support for this idea (Hussell 1972; Sanz 1999).

Ashmole (1963) hypothesized that seasonality – environmental characteristics of the time of year – is the primary driver of clutch size. Particularly, seasonality determines food abundance and population density (Ashmole 1963; Ricklefs 1980; Blondel 1985). As a follow up to Ashmole's hypothesis, Ricklefs (1980) examined clutch size in relation to actual evapotranspiration, which is proportional to primary productivity and fluctuates with seasonality. Ricklefs's results suggest that patterns of actual evapotranspiration are consistent with patterns of seasonality and clutch size. Evapotranspiration findings from Dunn et al. (2000) support both Ashmole and Ricklefs.

Predation rates have also been used to explain clutch size patterns. Skutch's (1948) hypothesis states that parents limit food trips to the nest to reduce predation risk, thus limiting clutch size. Bird populations typically experience higher mortality in temperate environments compared to tropical counterparts (Skutch 1948; Ricklefs 1980; Biancucci & Martin 2010), thus must rear more offspring to compensate (Skutch 1948). Studies support an energetic trade-off between predation avoidance and reproductive success (Cody 1966; Slagsvold 1982). However, predation rates also highly rely on nest site (Martin, Scott, & Menge 2000) and nest size (Biancucci & Martin 2010), which explains clutch size - predation patterns within a region, but not latitudinal patterns.

Yet another body of studies have explored determinants of variation in clutch size, in the context of physiology-based constraints on life history (Ricklefs & Wikelski 2002; Cooper et al. 2005). Most commonly, clutch size has been understood in the context of trade-offs among life history traits such as survival and reproduction. Life history theory informs studies of latitude trends in clutch size, such as noting that females allocate more to survival than reproduction at low latitudes (Lack 1947; Moreau 1944; Van Noordwijk & De Jong 1986). These studies have

assumed that clutch sizes are not constrained by environmental factors alone but vary in response to the species' life history traits, such as energetic trade-offs with adult survival rates (Martin et al. 2000; Ghalambor & Martin 2001), laying and incubation (Monaghan & Nager 1997), or multiple clutches (Cooper et al. 2005; Lundblad & Conway 2021).

Thus, the underlying drivers of latitudinal trends in clutch size are heavily theorized, but empirical support remains equivocal. While all the above explanations of clutch size trends are valid, perhaps there is yet another underlying mechanism or selection pressure that yields such latitudinally uniform results. Assumedly, such a mechanism would have to be present across all latitudes and have changed little to not at all over the past centuries.

B. Variation Within Latitude

Seasonal declines in clutch size have typically been explained by early breeders being more successful. According to Verhulst and Nilsson (2008), explanations of successful early breeders fall into two categories: quality effect and seasonal deterioration. The quality effect assumes that seasonal decline in clutch size is because individuals of higher quality breed before lower quality individuals, while (alternatively or in addition) seasonal deterioration of environmental conditions could lead to reduced clutch size. Ornithologists have proposed and tested numerous explanations for seasonal declines in clutch size (Table 1.1).

C. The Case for Photoperiod

While most studies of latitudinal trends have been comparative meta-analyses across species, most studies of seasonal declines in clutch size have been site specific and within species. Few studies have examined the ubiquitous latitudinal and seasonal patterns

simultaneously. When examined together, researchers have noted latitudinal trends in clutch size were composed of latitudinal trends in seasonal declines in clutch size (i.e., the clutch size - lay date relationship (Young 1994; Winkler et al. 2014; Dhondt et al. 2002). Specifically, as Winkler et al. (2014) argued, geographic variation in lay date accounts for latitudinal trends. In this study, we further examined the combination of date and latitude in relation to clutch size, given that together these are reliable and ubiquitous patterns (Dunn et al. 2000). We test the role an abiotic feature, which varies with latitude and date with greater predictability than biotic features.

Photoperiod (the duration of daylight, or the ratio of daylight to darkness) is the most predictable abiotic feature of the environment, so much so that nearly every organism responds in some way to it. Many birds use the annual solar cycle as a cue for seasonal events such as reproduction, migration, molt, and gonadal development (Kumar et al. 2010; Dixit & Singh 2011; Gaston et al. 2013; Huffeldt 2020). The photic environment across latitudinal gradients produces different breeding season conditions and lengths (Cooper et al. 2005; Dixit & Singh 2011) that inform many biotic factors including resource availability and competition between residential and migrating birds. However, there is accumulating evidence that the daily rate of change in photoperiod, rather than day length, is a more important cue for organisms in shaping seasonal rhythms (Kumar et al. 2010). Few studies attempt to examine the effects of minuscule changes (often less than a minute) of day-to-day light duration.

The temporal organization of behavioral and cellular events is controlled by circadian clocks, which enable organisms to synchronize behaviors and physiological processes with their external environment (Cassone & Menaker 1984; Bell-Pederson et al. 2005; Sahar & Sassone-Corsi 2012). Biological clocks are highly conserved across taxa and the functional output from clock systems are modified by photoperiod (Underwood et al. 2001; Zivkovic et al. 2000). The

central clock in the brain perceives light and synchronizes to photoperiod (reviewed by Bell-Pederson et al. 2005). The ovary has a clock that does not directly perceive light and instead responds to the temporal system of the brain through a variety of neuroendocrine pathways (Yasuo et al. 2003). The nature of the relationship between the brain and ovarian clocks, and how they are integrated, is unknown (see Pittendrigh 1972, Gwinner 1986 for formal descriptions).

One common model to describe the relationship between photoperiod and laying sequence assumes that the central oscillator in the brain entrains to light-dark cycles and directly drives other clocks and the rhythms of ovulation, creating central clock control (direct input from light receptors) of clutch size (Fraps 1970; Etches 1983). If this model is correct, then the laying sequence should respond to the duration of the photoperiod. Another model to describe the relationship between photoperiod and laying sequence assumes that the phase relationship between the central oscillator in the brain relative to, and based on feedback from, peripheral oscillators in the ovary provides peripheral clock (indirect input from systems regulating light receptors) regulation of clutch size (Underwood 2001; Zivkovic et al. 2000). If this model is correct, then the laying sequence should respond to the rate of seasonal changes in photoperiod.

Knowing that circadian and circannual inputs both influence clutch size outcomes, we analyze both in the context of just the laying period and attempt to resolve latitudinal and seasonal trends all with one model. Here we examine latitudinal and seasonal trends in clutch size within a species across their temperate breeding range. We take physiology-based hypotheses about clutch size variation and see how well they can account for latitudinal and seasonal trends. Biological clocks regulate the heterochronic dimensions of clutch size: timing of start, end, and rate of egg laying sequences (Perrin et al. 2006; Cooper et al. 2011). The model of

central clock control of clutch size predicts that clutch size responds to photoperiod duration, while the model of peripheral clock control of clutch size predicts that clutch size responds to the rate of change in photoperiod. We distinguish central and peripheral clock regulation of clutch size using breeding data spanning a wide range of natural and artificial photoperiod progressions for Eastern Bluebirds (*Sialia sialis*). If the central clock model is correct, we should see Eastern Bluebird clutch size be most strongly determined by daylength. If the peripheral clock model is correct, we should see Eastern Bluebird clutch size be most strongly determined by change in photoperiod.

II. Methods

A. Dataset

NestWatch is a nationwide monitoring program hosted by The Cornell Lab of Ornithology designed to track status, trends, and changes in the reproductive biology of birds. Volunteers gather information on breeding events, such as lay date, hatch date, and clutch size. This dataset is a subset of the full Nestwatch database focusing only on observations of Eastern Bluebirds (*Sialia sialis*). Eastern Bluebirds were chosen as a focal species due to their widespread abundance and popularity with birders. They take readily to nestboxes, so there are more nest records of Eastern Bluebirds than any other species in the US, and the records cover the extent of their US breeding range. This dataset contains 58,192 Eastern Bluebird nest records from 2000 - 2019. The breeding data spans a wide range of latitude, date, and photoperiod combinations.

B. Analysis

All analyses were performed in Program R Version 2023.06.0+421. We used the ‘suncalc’ package to get times for civil twilight (dawn and sunset) for each observation using the recorded latitude, longitude, and date. We used this information to calculate the day length (photoperiod) and change in day length from the previous date (change in photoperiod). We then ran 3 linear models explaining trends in clutch size: on the interaction of latitude and date, daylength duration, and rate of change in photoperiod:

- Model 1: Clutch size as a function of latitude and clutch initiation date (clutch size \sim lat + est_ld)
- Model 2: Clutch size as a function of day length of the clutch initiation date (clutch size \sim daylength)
- Model 3: Clutch size as a function of change in photoperiod of the clutch initiation date from the previous day. (clutch size \sim Δ photoperiod)

Finally, we compared the linear models based on the relative strength of evidence of each model using AIC (Akaike Information Criteria) values. We also compared R^2 values as an estimation of explained variance.

III. Results

The data span latitudes from 25.96 to 50.86°, with an average latitude of 37.84°. Clutch sizes ranged from 1 to 7, with an average clutch size of 4.5. Lay days spanned from day 8 (Jan 8th) to day 234 (about Aug 22), with the average observations around day 134 (about May 15). Photoperiods ranged from 9.96 to 17.29 hours, with the average photoperiod lasting 14.42 hours.

Meanwhile, Δ Photoperiod ranged from -2.98 to 3.68 minutes, with the average rate of change being 1.38 minutes.

As expected, average clutch size increased with latitude and decreased with lay date. Clutch size also increased with a positive change in photoperiod. Daylength shows fluctuations across durations, indicating a non-linear effect in the model. While all models are close in robustness, we found that change in photoperiod (Model 3) is a better linear predictor of clutch size than day length or latitude + date in temperate-breeding Eastern Bluebirds. Clutch size increased by 0.25 eggs with daily change in photoperiod. Model 3 had the lowest AIC (122701.8), highest log-likelihood (-61347.90), as well as the highest R^2 (0.16), lending support to the peripheral clock control hypothesis. All model results are summarized in Table 1.2.

IV. Discussion

Our findings support the idea that peripheral clock control mechanisms - the mechanisms controlling ovulation in laying birds - are most likely responding to the daily changes in photoperiod. Although latitude and date are human constructs representing geography and time in a way relevant for people, these are better predictors than daylength. Within our dataset, there was no way to account for the number of clutches that might have been laid by a single breeding pair; re-nesting could account for some variability in the daylength model results. Overall, our findings suggest that songbirds perceive small changes in photoperiod, and these can proximately regulate clutch size.

The annual cycle of photoperiod are cues that shape phenology, such as seasonal events of reproduction, migration, and molt (Gwinner, 1986; Kumar et al. 2010). Our findings suggest these cues also shape clutch size through the onset and termination of egg laying. Our findings

could also be explained by the Yule-Simpson paradox - a mathematical paradox that disappears when the causal relations are considered (Blyth 1972). When taken together, latitudinal and seasonal trends in clutch size resemble a Yule-Simpson paradox because clutch size declines with date within sites but increases with date across sites arranged along a latitudinal gradient. Change in photoperiod is a more parsimonious way to describe clutch size patterns and doing so may help figure out the underlying cause.

Our results suggest the need to disregard latitude and date as human constructs and see the utility in examining patterns in relation to natural phenomena, such as change in photoperiod. Since we found change in photoperiod to be the best predictor of clutch size, we also suggest the need to examine clutch size differently. Clutch size is a life history trait that is typically viewed as a determinate number inherent to the species rather than a continuum controlled by adult body mass (Hussell 1972; Jetz et al. 2008; Haywood 2013a), conditions and resources for egg and embryo production (Ardia et al. 2006; Cooper et al. 2011; Haywood 2013b; Lundblad & Conway 2021), and photoperiod-stimulated ovary production cycle (Zivkovic et al. 2000; Cooper et al. 2011; Voss & Cooper 2013), among other neuroendocrine factors. To shift to a mechanistic approach, we should examine clutch dynamics within its heterochronic dimensions, namely as a sequence of phenological events (egg laying) with a start time, a frequency, and a termination time. Haywood 2013b (and pointed out by Voss and Cooper 2013) demonstrated that the trait (or suite of traits) under selection is not the number of eggs in a clutch (an ordinal trait that we measure quantitatively) but the physiological mechanisms controlling the laying sequence. Birds have many neuroendocrine functions that activate and regulate in response to light. Pineal glands are highly sensitive photoreceptors that signal circadian endocrine functions like melatonin production and ovulation (Gaston 1968; Kumar et al. 2010; Gaston et al. 2013). Biological

clocks regulate the heterochronic dimensions of clutch size through the timing of start, end, and rate of egg laying sequences (Cooper et al. 2009). The temporal organization of behavioral and cellular events is controlled by circadian clocks, which enable organisms to synchronize behaviors and physiological processes with their external environment. Therefore, it makes sense that birds are highly sensitive to changes in light, no matter how minute.

Viewing selection on clutch size as functionally linked to the phenology and heterochrony of egg-laying has implications for several lines of research, including predicting demographic and evolutionary consequences of climate change and integrating the role of biological clocks, and comparative chronobiology, into life history evolution. With regard to climate change, better understanding the mechanisms by which changes in photoperiod cue clutch size might facilitate predicting clutch size as birds shift the timing of clutch initiation (Crick et al 1995). Songbirds appear to shift laying dates to track temperature and consequently have been laying earlier in the annual photoperiodic cycle as global temperatures rise (Dunn and Winkler 2010). Thus, better knowledge of the mechanisms of ovulatory control may help elucidate why a very strong linkage between earlier lay dates and larger clutches does not extrapolate to lead to larger clutches when the entire population undergoes a shift toward laying earlier (Winkler et al 2000). Our findings should encourage research about optimal clutch size to expand to include the link to timing of clutch initiation; studies on the photoperiodic regulation of clutch size are newly interesting to evolutionary ecologists as well as physiologists. In addition, while our hypotheses are limited by the assumption of 100% plasticity based on physiological controls, this is unlikely the full picture. Thus, future studies should test the specific degree of plasticity with common garden experiments.

VI. Tables

Table 1.1. Sample of studies of different causes of seasonal decline in clutch size.

Cause for early breeders laying larger clutches	Reference
Greater access to higher quantity of food	Schoech et al. 2004 Ardia et al. 2006
Greater access to higher quality of food	Twining et al. 2018
Access to higher quality mates	Kirkpatrick et al. 1990
Access to limited number of mates	Ferretti and Winkler 2009
Access to higher quality nesting sites	Rosvall 2008
More time for subsequent attempts	Monroe et al. 2008 Morrison et al. 2019
No time for delay because of high mortality rates	Goutis and Winkler 1992
Quality of breeding female	Winkler et al. 2020

Table 1.2: Model statistical summaries ranked by best AIC value, R^2 , and log-likelihood (LL).

Model	variable	β	se	p-value	R^2	K	AIC	Δ_AIC	w	LL
Model 3	Intercept	4.13	0.00	<2e-16	0.16	3	122701.8	0.00	1	-61347.90
	Δ Photoperiod	0.25	0.00	<2e-16						
Model 1	Intercept	5.15	0.03	<2e-16	0.15	4	123418.0	716.19	0	-61704.99
	Latitude	0.01	0.00	<2e-16						
	Lay Day	-0.009	0.00	<2e-16						
Model 2	Intercept	7.59	0.04	<2e-16	0.08	3	128045.9	5344.12	0	-64019.96
	Daylength	-0.22	0.00	-71.07						

VII. Figures

Figure 1.1: Eastern Bluebird clutch size as a function of photoperiod change, showing that clutch size increases as the day lengths get longer than the previous day.

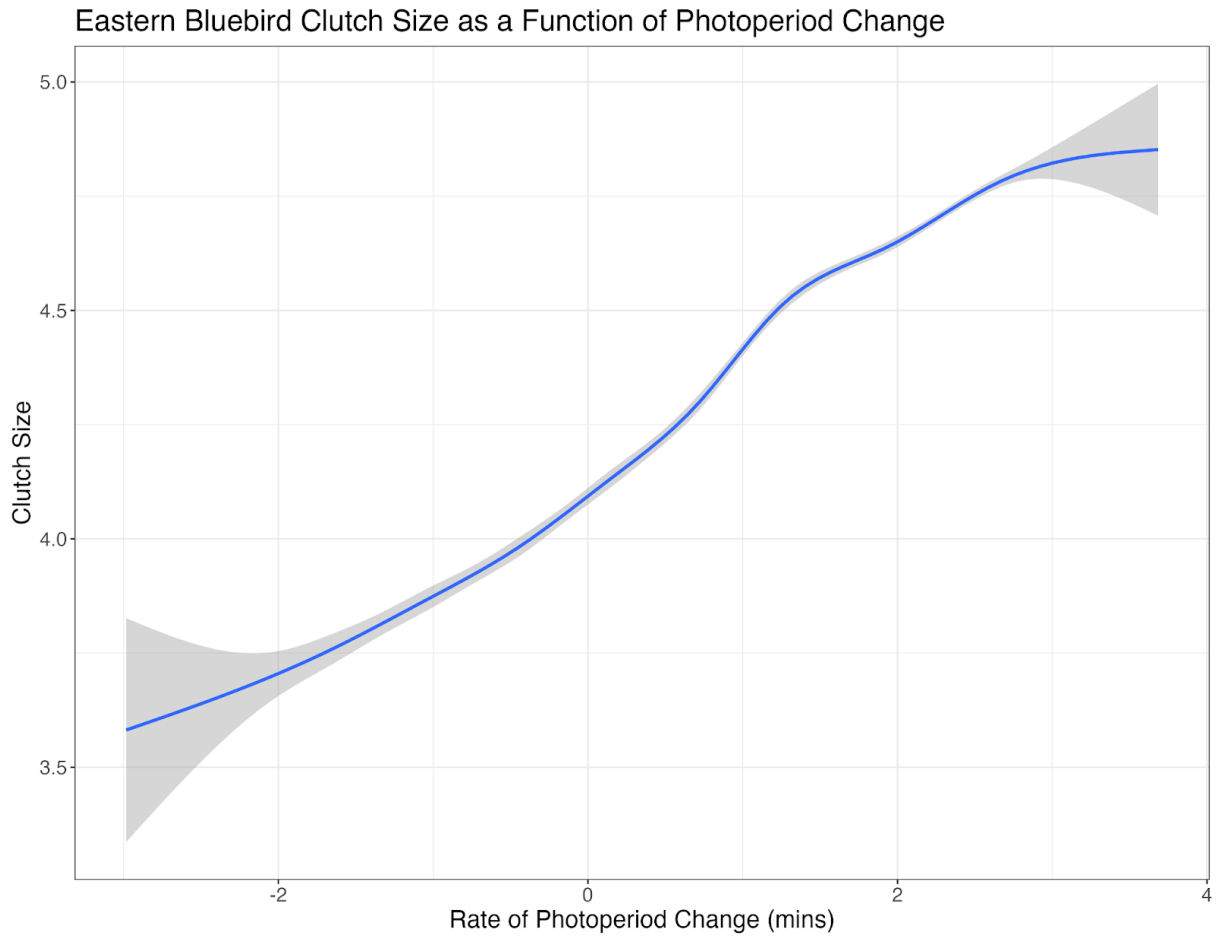


Figure 1.2: Eastern Bluebird clutch size as a function of lay date, showing that clutch size decreases relative to the lay date, and that clutch size is smaller in lower latitudes.

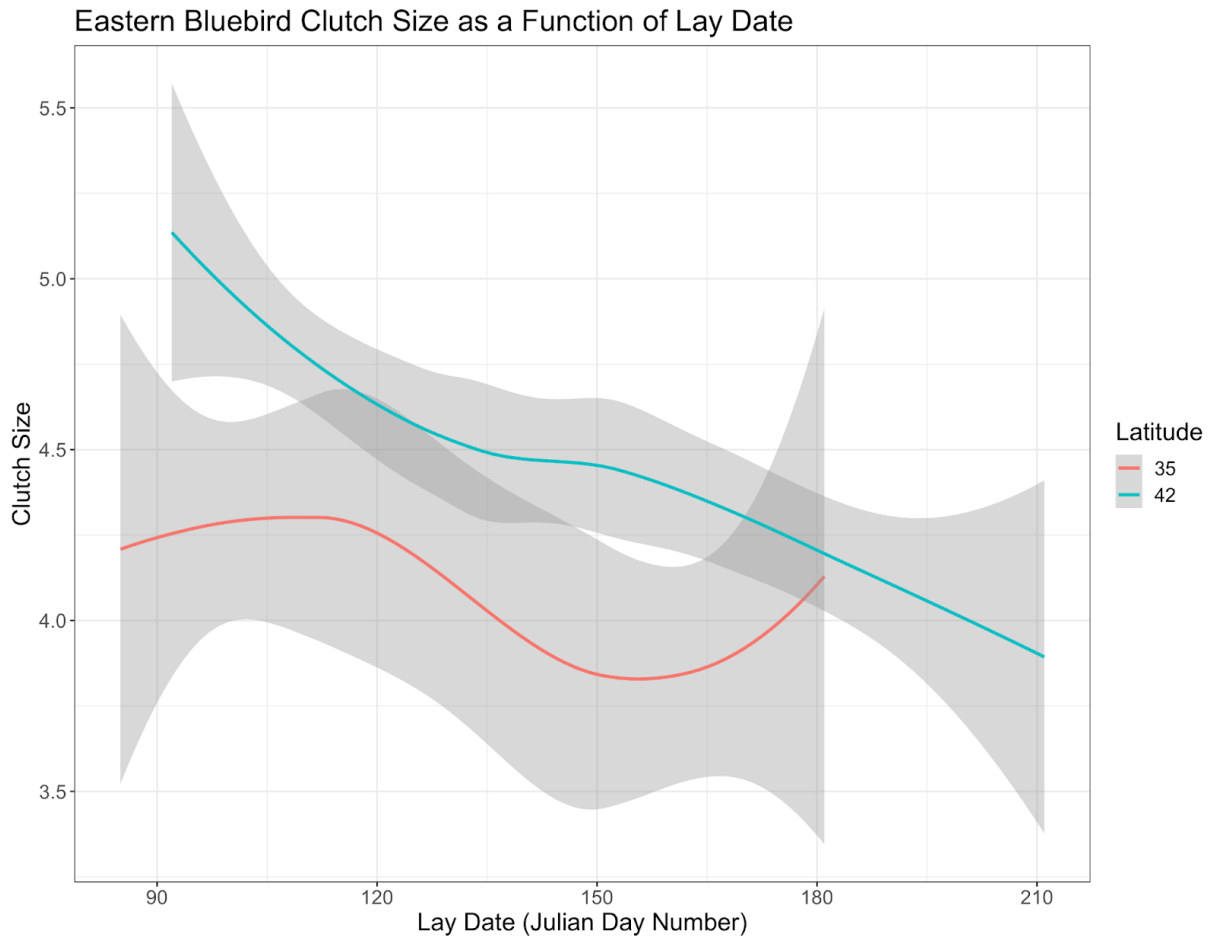


Figure 1.3: Eastern Bluebird clutch size as a function of daylength, showing non-linear variability in clutch size that does not follow a particular daylength pattern.

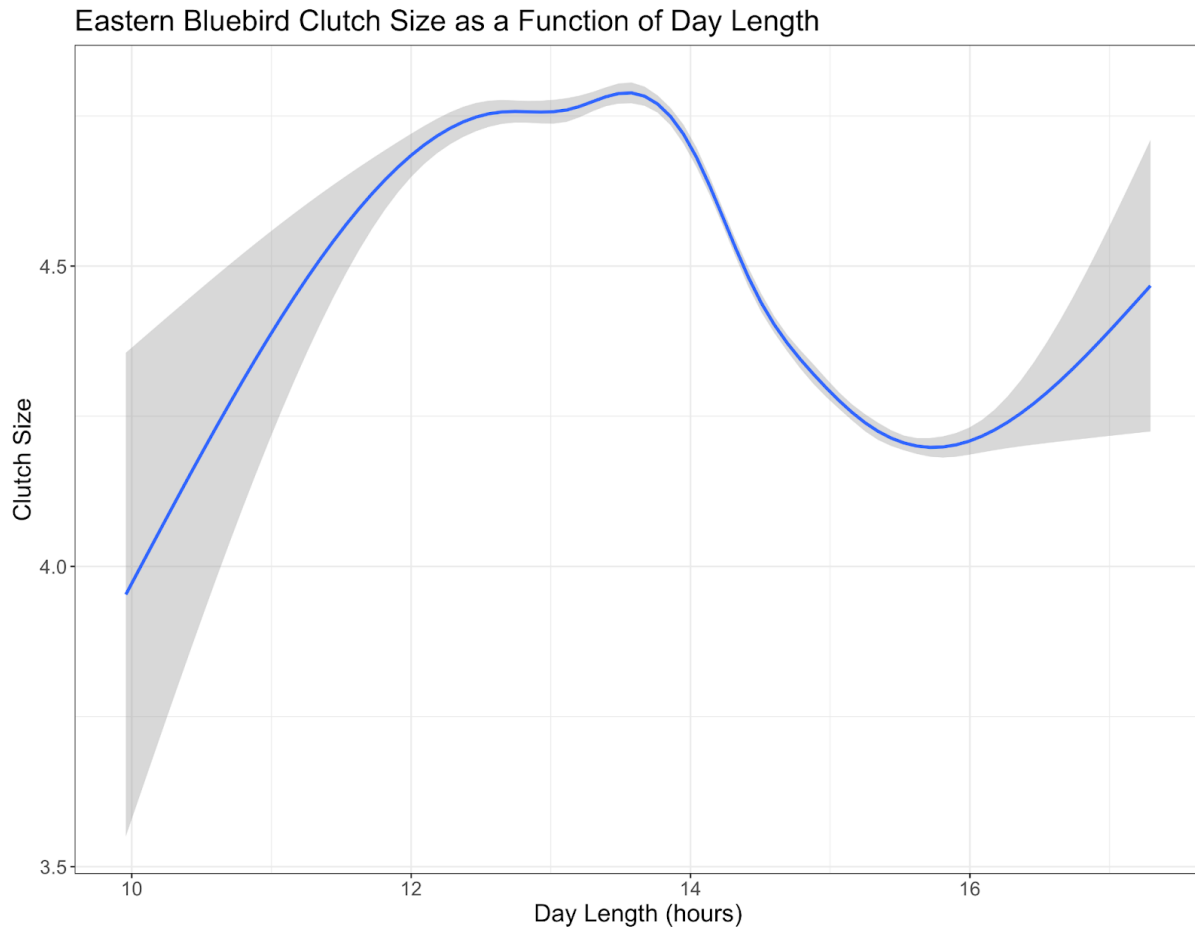


Figure 1.4: Eastern Bluebird clutch size as a function of daily photoperiod change using predicted clutch size values from the linear model. Clutch size increases with a positive change in photoperiod from the previous day.

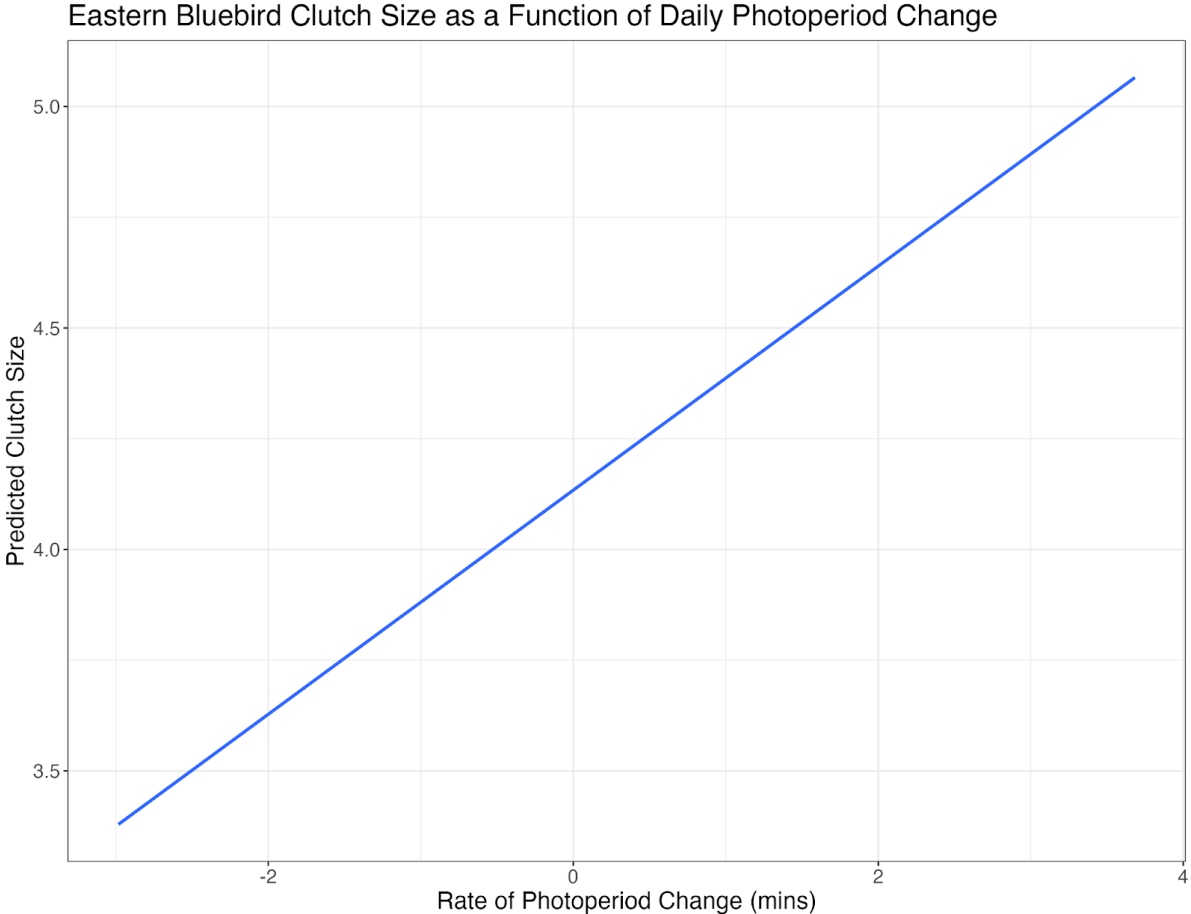


Figure 1.5: Eastern bluebird clutch size as a function of lay day using predicted clutch size values from the linear model.

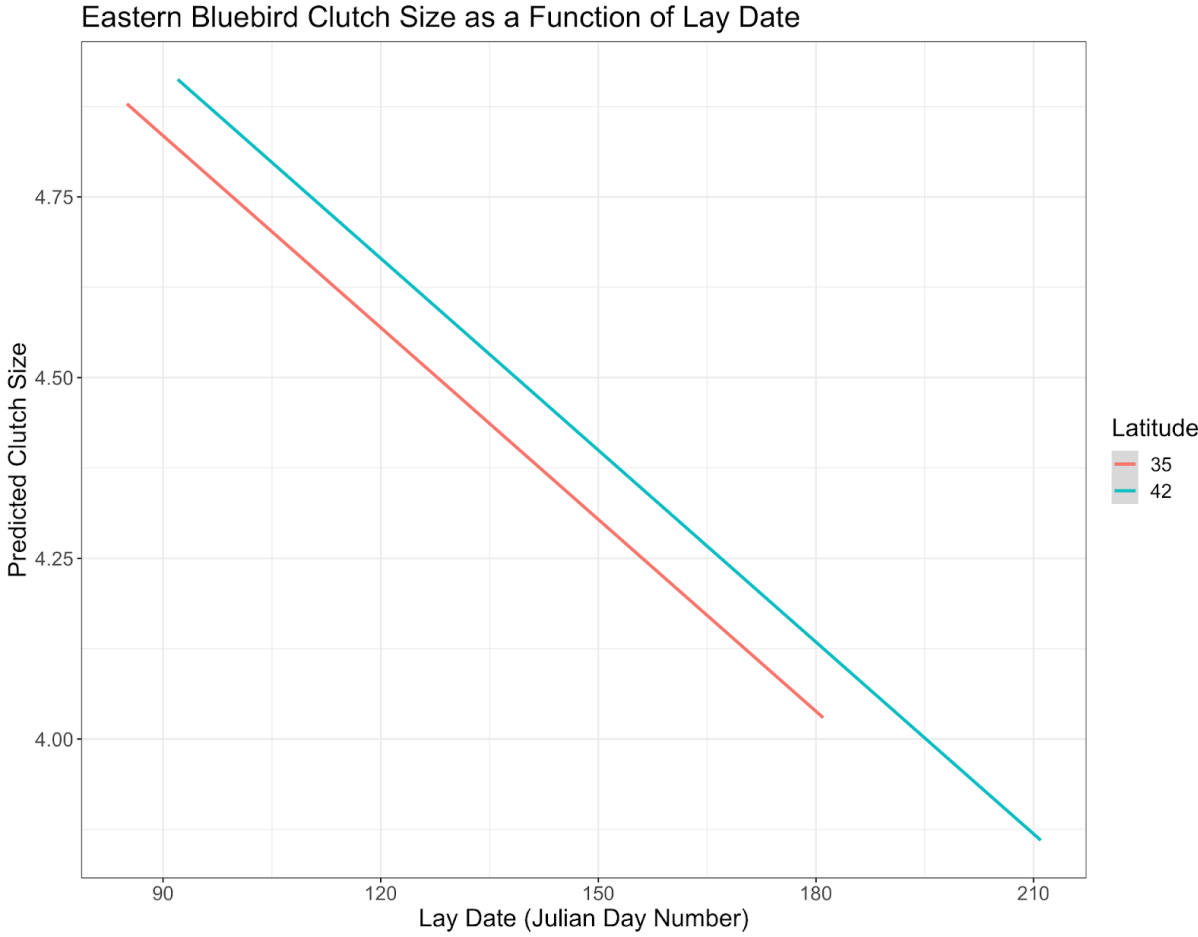
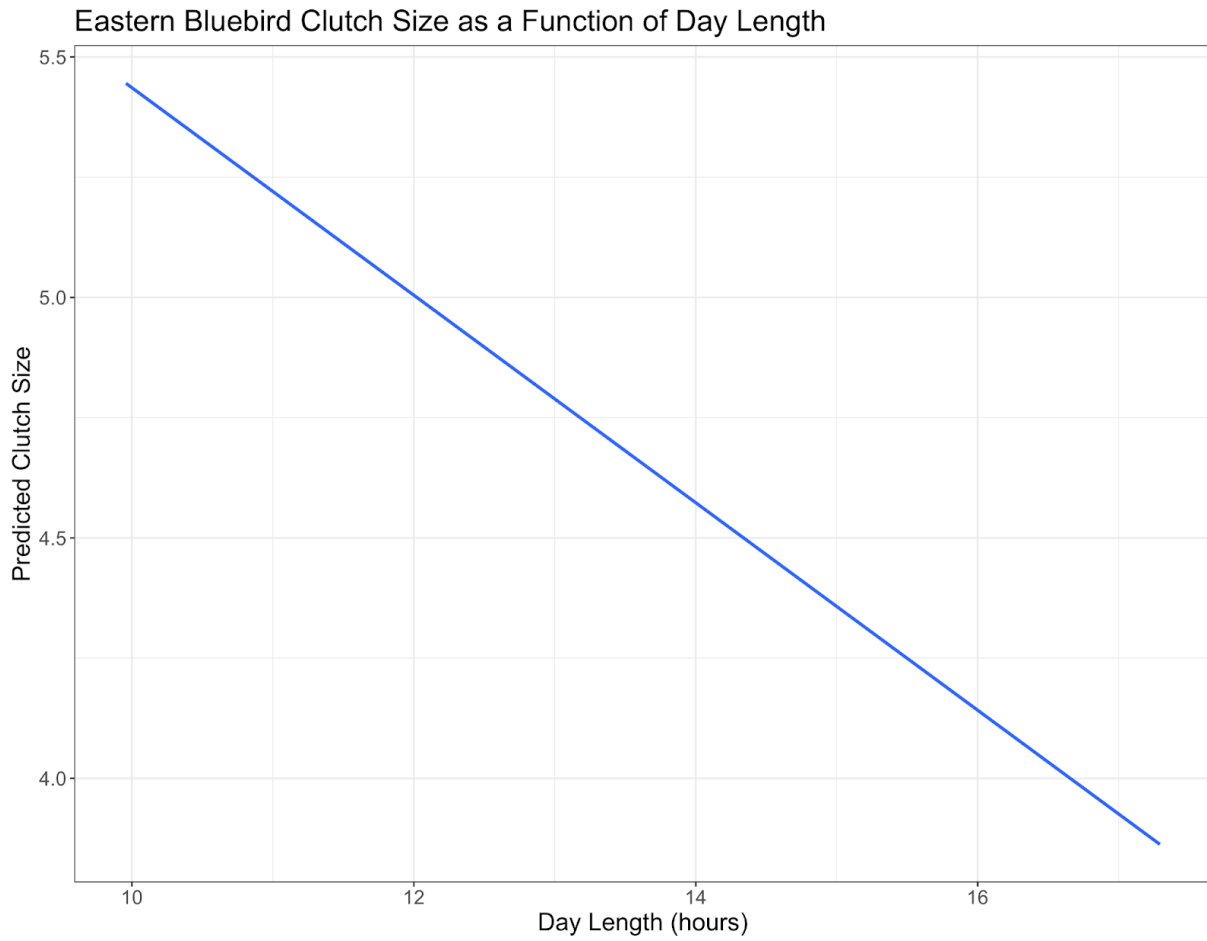


Figure 1.6: Eastern Bluebird clutch size as a function of daylength, using predicted clutch size values from the linear model.



CHAPTER 2: The Role of Artificial Light at Night on Metabolic Health and Physical Development of Barn Swallow Nestlings.

I. Introduction

Daily and seasonal changes in photoperiod are ubiquitous cues used by virtually all life on Earth (Foster & Kreitzman 2004; Dominoni et al. 2013; Hufeldt 2020). Through the expression of clock genes and neuro-endocrine signals, the timing of life-cycle events is synchronized with local photoperiodic environments. Phenology - the timing of life cycle events - is heavily influenced by circannual light and dark (Dominoni et al. 2013; Newport et al. 2014). Birds rely on circannual and circadian light cues for migration and reproduction (Dominoni et al 2013; Ouyang et al. 2015). Photoperiod-based cues affect several aspects of reproduction, such as arrival to reproduction grounds (aka, migrating timing) (Van Doren et al. 2017), gonad development (Henare et al. 2011; Dominoni, Quetting, & Partecke 2013), ovulation (Dominoni 2015), and foraging (Titulaer et al. 2012; Newport et al. 2014; Raap et al. 2016a).

Because of its rapid development and spread, artificial light at night (hereafter ALAN) has dramatically altered natural photoperiod, especially nightscapes. ALAN includes direct lighting and skyglow, which refers to the scattering of light particles into the atmosphere. ALAN is a sensory pollutant because skyglow obscures the visibility of stars and homogenizes nightscapes which can disrupt avian navigation, while direct lighting and skyglow disrupt interpretation of natural photoperiod cues (Longcore & Rich 2004; Gaston et al. 2013; Newport et al. 2014; Gaston et al. 2021; Liu et al. 2022). ALAN alters the way birds perceive light (Hufeldt 2020), and thus alters timing of phenology (Longcore & Rich 2004; Da Silva et al. 2015). For example, altered onset of dawn song in diurnal species (Dominoni et al. 2013; Da Silva et al. 2015; Derryberry 2017), extended foraging periods (Dominoni et al. 2013; Newport

et al. 2014; Stracey et al. 2014; Russ et al. 2015), earlier gonad development (Dominoni, Quetting, & Partecke 2013; Da Silva et al. 2015), and interrupted sleep (Raap et al. 2016a) have all been documented responses of wild songbirds to ALAN. In the past decade, ALAN increased between 6 - 10% each year, as reported by citizen scientists, and as much as 2.2% each year by satellite measures of skyglow (Da Silva et al. 2015; Kyba et al. 2023). Over one-third of the world cannot see the Milky Way (Falchi et al. 2016; Gaston et al. 2021), including 60% of Europeans and 80% of North Americans (Falchi et al. 2016). At this rate, ALAN will soon be prevalent worldwide (Newport et al. 2014).

Ornithologists have done research on ALAN-induced mortality at individual, population, and ecosystem levels (Gaston et al. 2021); changes in navigation and migration lead to building collisions (Van Doren et al. 2021) and decreased ability to avoid predators (Newport et al. 2014; Swaddle et al. 2015). Despite the pervasiveness of ALAN and the myriad of cascading effects, understanding of sub-lethal effects of this form of global anthropogenic change on avian reproductive health and development remains poor.

A. ALAN's Impact on Avian Reproduction

When photic input becomes misaligned with environmental conditions (eg., nest material, food availability, temperature, etc.), birds may experience a decrease in individual health and/or overall fitness (Huffeldt 2020; Senzaki et al. 2020; Pharr et al. 2023). Since birds rely on photoperiod to time their reproduction, ALAN may affect the physiology and metabolism of parents and nestlings (Liu et al. 2022).

Previous studies provide examples of birds under urban lighting regimes showcasing different behavioral and hormonal phenotypes than their rural counterparts. Experimental

research on common songbirds, in suburban nest boxes, experimentally lit forests, and captive in the lab, showed that ALAN causes sleep interruption (Ouyang et al. 2015; Raap et al. 2015), increased extra-pair paternity (Kempnaers et al. 2010), earlier lay dates (Kempnaers et al. 2010), and earlier onset of daily activities such as dawn chorus and foraging (Raap et al. 2015; De Jong et al. 2016; Dominoni et al. 2022). Because ALAN extends adults' foraging period, ALAN may also indirectly impact the amount of nutrition chicks receive, which can factor into nestling success (Stracey et al. 2014; Lamb et al. 2016). Based on these studies, we can assume that circadian rhythm - an organism's internal clock that is governed by daily light and dark cycles - is being interrupted, causing stress, sleep deprivation, and behavioral changes. Behavioral changes can also result in physiological changes. ALAN is also associated with increased markers of stress (eg., corticosterones) (Ouyang et al. 2015; Lamb et al. 2016), decreased melatonin levels (De Jong et al. 2016), and differences in clock gene expression (Dominoni et al. 2022).

Some focus has also been given to examining nestling responses to ALAN. Many studies find that ALAN affects the overall physiological condition of nestlings (Ouyang et al. 2015; Swaddle et al. 2015; Raap et al. 2016b). For example, nestlings exposed to ALAN had higher levels of stress hormones and were less likely to fledge (Ouyang et al. 2015; Lamb et al. 2016; Raap et al. 2016b). Behaviorally, ALAN also caused chicks to beg throughout the night (Titulaer et al. 2012; Soler et al. 2014; Raap et al. 2016b). Increased nighttime begging could lead to decreased body mass because energy would be directed elsewhere (Raap, Pinxten, & Eens 2016). ALAN during the incubation period resulted in lower body mass at hatching (Swaddle et al. 2015). Continued ALAN exposure caused nestlings to gain mass more slowly (Ouyang et al. 2015; Lamb et al. 2016; Raap et al. 2016b). Nestlings with higher body condition and less stress

were more likely to fledge and survive after fledging (Ouyang et al. 2015; Lamb et al. 2016). In addition, increased stress markers and behavior change in parents impact nestling survival.

B. The Role of Glucose

Compared to mammals of similar body mass, birds naturally have a much higher blood glucose level, yet they experience no hyperglycemic effects (Beuchat & Chong 1998; Braun & Sweazea 2008; Li 2017). Under typical circumstances, birds store unused nutrients, repair tissues, and recharge their bodies when they rest at night (Raap et al. 2015). In birds, high demand for blood sugar is met by gluconeogenesis from the liver, rather than insulin (Li 2017). When a bird is stressed, it uses circulating blood glucose for energy, so the demand for glucose increases the more stress increases. If liver glycogen stores are insufficient to meet the energy demand of the stress response, protein will be used instead to fuel gluconeogenesis (Li 2017). Protein is needed to fuel the immune system and energetic functions, such as flight (Ardia 2006; Kaliński et al. 2014, Li 2017). Altricial nestlings in particular experience high energy demands during growth; in a stressful environment, rapid growth could outpace glucose delivery and thus cause protein to be redirected for energy production. Protein also affects developing anatomy such as keratin and body mass (Ardia 2006; Downs et al. 2009; Kaliński et al. 2014).

ALAN may be a novel environmental stressor triggering gluconeogenesis in nestlings. By taking blood samples from American kestrel nestlings, Ardia (2006) found a direct relationship between glycated hemoglobin and structural growth, thus providing information about body condition through glucose sampling. Glycated hemoglobin correlated to physiologically elevated blood glucose (Ardia 2006), indicating that there was excess glucose in the bloodstream that was not needed for the current metabolic demand. Because ALAN alters circadian rhythm, and blood

glucose is partially regulated by circadian rhythm (Ruiter et al. 2003; Downs et al. 2009), daily blood glucose concentrations may similarly be altered by ALAN. In other words, a longer photoperiod, or artificial photoperiod as a stress signal, may increase blood glucose concentrations. Studies on nestlings have found a positive relationship between glucose and degree of urbanization (Kaliński et al. 2014) and an inverse relationship between body mass and glucose (Braun & Sweazea 2008; Lill 2011; Kaliński et al. 2014). High glucose also correlates to low fledging success (Kaliński et al. 2014). Therefore, taking blood glucose measurements could be a stand-in for typical metabolic stress measurements (i.e., corticosterones).

Therefore, chicks exposed to ALAN might have smaller bodies and poor metabolic health. High intensity or prolonged exposure to ALAN may cause metabolic diseases by increasing blood glucose levels and related hypothalamus and pituitary hormones above the avian norm (Reinert & Wilson 1996; Yasuo & Yoshimura 2009). While many urban ALAN studies have attempted to measure different blood indices on urban bird populations, few are experimental, and even fewer have focused on understanding the potential for metabolic disease. There are only a handful of papers studying avian glucose concentration, and a majority focus on poultry or captive species (John et al. 1989; Beauchat & Chong 1998; Ardia 2006; Maitra et al. 2008; Kaliński et al. 2014).

To examine the potential sublethal consequences of ALAN exposure on chick development, I carried out a field experiment on wild, free-ranging songbird nestlings. I measured the physical and physiological development of chicks experimentally exposed to ALAN and in controlled conditions absent of ALAN. I expected ALAN exposure to function as a stressor on nestlings, resulting in more glucose circulating in the bloodstream and causing less protein to be available for accumulating mass or for skeletal and keratin-based growth. The goal

of this research is to examine if ALAN is an environmental stressor on nestlings. I predict that nestlings exposed to ALAN will have higher blood glucose and slower growth.

II. Methods

A. Focal Species

I chose barn swallow (*Hirundo rustica*) nestlings as the focal species for this experiment. Barn swallows (BARS) are a common, diurnal, aerial insectivore found in the Americas, Europe, Asia, and Africa, and they are present in all major flyways. While barn swallows are currently considered a species of least concern (IUCN), populations are declining across most of their range (Nebel et al. 2010) due to pesticides and harmful agricultural practices (Ambrosini et al. 2012; Spiller & Dettmers 2019; Li et al. 2020). Barn swallow decline may also be impacted by loss of nesting sites as old wooden barns are replaced with metal ones (Spiller & Dettmers 2019). ALAN is not currently considered a cause for Barn Swallow decline, so this further makes them an appropriate species for a controlled field experiment.

Barn swallows nest on built wooden structures which makes it easy to construct an experimental setup. Our selected breeding population nests on the beams in an old, wooden barn in rural Snow Camp, NC (population <6,000). We chose this location so that the only artificial light interference would be from those we added to the system. Barn swallows have altricial nestlings that take around 15 days to fledge (Fernaz et al. 2012). Both parents contribute to raising offspring. Variability in altricial nestling growth can be affected through ecological stressors (Ricklefs 1993; Fernaz et al. 2012) - such as ALAN - and could lead to developmental tradeoffs (Fernaz et al. 2012).

B. Field Experiment

During the breeding seasons of 2020 - 2022, I conducted a field experiment to test the effects of ALAN on wild barn swallow nestlings. The barn was open on two sides allowing nests to experience natural photoperiod. I randomly selected nests to be illuminated with 3000 K, “warm white” LED lights. (Note that “warm white” describes the color spectrum of the lights, not the temperature.) Control nests received the same light set-up, but the lights were not turned on. I monitored lux levels at night with a light meter throughout the experiment, ensuring a true difference between light treatments and natural darkness. Lux measurements were taken once a month and were consistent throughout the experiment. Measuring with a light meter, control nests measured 0.0 lux, while treatment nests ranged from 1.6 – 20.2 lux. Lower-level measures resulted from the light meter being 1 ft away from the cup of the nest. Higher-level measures resulted from the light meter being placed directly into the cup of the nest. The difference between these types of light meter measures is to account for scenarios of nestlings being directly exposed to ALAN and nestlings being blocked or partially blocked by a roosting parent. These artificial light levels are greater than that of the full moon (~ 0.3 lux) and comparable to street lighting (3 - 21 lux) (Newport et al. 2014). Effects of ALAN can be detected at low levels (Dominoni et al. 2022). Lower-level lights are also more prevalent across a global scale than higher intensities (Gaston et al. 2021). I placed lights on a timer, and the lights remained on from sunset to sunrise throughout the April to July breeding season.

Due to university policies regarding lockdown restrictions at the start of the covid-19 pandemic in 2020, the lights were not set up until mid-May, after some of the first broods had already hatched. During 2021, the lights were first turned on in early April before the barn swallows arrived. I observed a change in nest selection due to the lights – adults avoided lit nests

(as is consistent with findings in Longcore & Rich 2004), thus I altered protocol to turn lights on only after the clutch had been completed. I also changed the type of lights from LED Christmas string lights to flat-string LED lights to reduce rat snake predation. I ensured the chosen lights emitted the same color temperature and lux.

I monitored nests for lay date (estimated when possible in 2020), hatch date (estimated when possible in 2020), brood size, predation, and nestling survival. I considered a nest predated when all eggs went missing from a nest overnight; I knew there was a rat snake in the barn and made efforts to exclude it from nests or capture and relocate it. I monitored daily throughout the breeding season. I marked nestlings' nails with nail polish to distinguish individuals in a nest. On day 10 post-hatch, I banded nestlings with size 0 metal bands (sub-permit #23822-G). I grouped nestling measurements into three categories: morphological, feathers, and physiological. For morphological measurements, I recorded mass, head length, bill length, wing chord, tarsus length. I used a digital scale to measure mass to a tenth of a gram, and I used calipers to measure to the nearest millimeter. For feather measurements, I physically measured feathers to the 100th millimeter with a wing chord ruler. I measured feathers as soon as they erupted from the pin sheath and recorded lengths of the 1st primary, 5th primary, 9th primary, an outer tail feather, and a head feather. I also took standardized photographs every day the nestlings were handled for a visual representation of pin and feather growth progression. Each photo consisted of the nestling lying on its stomach, a ruler for size, and an index card with the date and nestling ID (Figure 2.1). For physiological measurements, I measured fat and blood glucose. I visually examined the furcular depression, intestines, and abdomen for yellow, fatty deposits to determine fat score. I took glucose measurements in the field with a OneTouch UltraMini handheld glucometer, measured in dg/mL. I measured blood glucose every other day, just after sunrise,

until fledge. A drop of blood was taken from the left brachial artery into a capillary tube (< 25ul) to be inserted into the glucometer for an instant reading. I took all measurements of barn swallow nestlings starting on their hatch date (Day 1) and continuing every other day until fledge (approx. Day 20) in accordance with IACUC protocol #19-763.

C. Statistical Analysis

I considered an alpha of 0.05 to be the level of significance. I considered the nest to be my sample unit. I used t-tests to verify that nests randomly assigned to treatment and control groups did not differ in key features such as incubation period or clutch size. For my analysis of nestlings, I ran a Principal Components Analysis (PCA) on all morphological (excluding mass) and feather variables to test their degree of correlation. I used Varimax rotations on the PCA. I then used linear mixed models on the most strongly correlated rotated PCA loading scores (Table 2.3), as well as on the physiological variables and standardized photo scores. Each linear mixed model included random effects (Nest ID), repeated measures (Chick ID), and age as covariates. Although I did not directly measure adult behavior or stress, the random effects factor in my models is important for controlling for genetic and parental care effects. Year was excluded as a covariate due to 1) low nest sample size and 2) running a linear mixed model analyses to check if year has an effect across treatments and finding no significant effect. For body condition index (BCI), I ran two ordinary least squares (OLS) models using mass and skeletal growth variables - right wing chord and right tarsus. I used the residuals of these OLS models as indices of BCI.

I assigned each standardized photo a categorical score based on the developmental stage of the feathers for five regions of the body: head-nape, back, wings, thighs, and tail. Developmental stage scores were created based on the standard developmental progression of

Barn Swallow nestlings as described by Fernaz et al. 2012 (Table 2.1). The developmental thresholds of visible subdermal pin tracks (sub) and pins emerging through the skin (em) are considered the most reliable aging indicator (Fernaz et al. 2012). These scores were then modeled to determine the age and mass at which chicks reach these developmental thresholds on different areas of the body.

All analyses were performed in Program R Version 2023.06.0+421 (R Core Team 2023). I performed the linear mixed models using the “nlme” package (Pinheiro, Bates, & R Core Team 2023). I performed the PCA analysis using “corr” (Kuhn, Jackson, & Cimentada 2022) and “FactoMineR” (Le, Josse, & Husson 2008) packages.

III. Results

A. Nest Monitoring

My final sample size was 32 nests (containing 353 observations of 101 chicks) for the control group and 16 nests (containing 187 observations of 58 chicks) for the treatment group. Using two sample t-tests, I found that control and treatment nests did not differ in clutch size ($t = -1.01$, $p = 0.32$) or brood size ($t = -0.78$, $p = 0.44$). Although 18 days seems notably different than 15.4 days, control and treatment nests did not differ in incubation period due to a large standard error ($se = 1.31$, $t = 1.95$, $p = 0.08$). Control and treatment nests did not differ in percentage of eggs that hatched ($t = -0.98$, $p = 0.34$) or percent of chicks that survived to the fledgling stage ($t = 1.83$, $p = 0.08$). Predation was equal between treatment and control, with 13 predation events each. See Table 2.2 for all nest monitoring statistics.

B. PCA and Morphological Development

From the PCA analysis, I found that nestlings measurement variables could be split into two major components, and that these two components made up most of the variation within the dataset. Component 1 is feathers (all excluding tail feather) and makes up 77.1% of explained variances. Component 2 is morphology (excluding left wing and left tarsus due to low sample size) and makes up 11.6% of explained variances. Remaining variances are split between 8 other Components. Physiological variables (fat and blood glucose) were not strongly correlated to any other variables. See Table 2.3 and Figures 2.3 – 2.4.

I ran linear mixed models with random effects and repeated measures on Components 1 and 2. Results from the Component 1 model shows that there was no difference in feather development between control and treatment ($b = 0.87 \pm 0.52$, $t = 1.65$, $p = 0.10$, Table 2.4). Since tail feathers seemed to not weigh heavily on Component 1, I ran a separate linear mixed model for tail feather length. I found that tail feather length of nestlings in the light treatment grew on average 2.12 mm longer than control chicks ($b = 2.12 \pm 0.50$, $t = 4.28$, $p = 0.00$, Table 2.7, Figure 2.6). Results from the Component 2 model show that treatment nestlings morphologically developed at a slower pace than control nestlings ($b = -0.55 \pm 0.26$, $t = -2.12$, $p = 0.03$, Table 2.5). Finding mass to be a highly significant effect on its own and using it as a variable in the photo score analysis, I separated it from the other morphological variables making up Component 2. I found that chick body mass averaged about 1g lighter in treatment than control nests ($b = -1.02 \pm 0.4$, $t = -2.55$, $p = 0.01$, Table 2.6, Figure 2.5). Both wing ($b = 0.02 \pm 0.03$, $t = 0.91$, $p = 0.37$) and tarsus ($b = -0.01 \pm 0.03$, $t = -0.30$, $p = 0.76$) BCI models were found to be insignificant (Table 2.11).

C. Standardized Photo Scores

For all age models, there was no difference in stages of feather development between treatment and controls. For mass, there was little difference in patterns of feather development between treatment and control chicks; the only exception was that treatment chicks were around 1.5 to 3.5g lighter than control chicks when pin feathers first emerged ($b = -2.52 \pm 1.13$, $t = -2.23$, $p = 0.04$). See Tables 2.8 – 2.10 and Figure 2.7.

D. Physiological Measurements

Fat score did not differ between control and treatment nests ($b = -0.001 \pm 0.03$, $t = -0.04$, $p = 0.97$, Table 20). Blood glucose levels do not differ between control and treatment nests ($b = 14.92 \pm 10.69$, $t = 1.40$, $p = 0.17$, Table 2.12).

E. Additional Observation: Asymmetry

I initially only measured the right side for wing chord and tarsus length. However, I observed a handful of cases of severe wing asymmetry in ALAN nestlings where one wing was substantially more developed than the other (Figure 2.2). Subsequently, I measured wing and tarsus length on both right and left sides of all nestlings (control $n = 8$ nests; treatment $n = 9$ nests). I calculated wing asymmetry by subtracting the length of the left wing from the length of the right wing. Asymmetry in wing chord length did not differ between treatment and control nests ($b = -0.55 \pm 0.75$, $t = -0.73$, $p = 0.47$). Similarly, asymmetry in tarsus length did not differ between treatment and control nests ($b = 0.12 \pm 0.12$, $t = 0.96$, $p = 0.35$). See Table 2.13.

IV. Discussion

I experimentally assessed the potential morphological and physiological effects of ALAN exposure on barn swallow nestlings in the wild. Contrary to other studies (Kaliński et al. 2014; Ouyang et al. 2015; Lamb et al. 2016), nest success, nestling body condition, and nestling physiology did not differ between nests exposed to ALAN (treatment) and natural photoperiod (control). Instead, nestlings appeared to maintain body condition and metabolic health. Yet, sublethal effects of ALAN were apparent in body mass and the rate of morphological development. Relative to control nestlings, those exposed to ALAN lagged behind in body mass by about a day and skeletally developed slower. Our findings were like several other studies that also found slow mass gain in nestlings exposed to ALAN (Ouyang et al. 2015; Lamb et al. 2016; Raap et al. 2016b). Lower mass treatment nestlings are consistent with observations of ALAN exposure associated with chick begging throughout the night (Titulaer et al. 2012; Soler et al. 2014; Raap et al. 2016b). In 2021, nests were also exposed to ALAN during the incubation period, which can result in lower body mass at hatching (Swaddle et al. 2015).

In addition, treatment nestlings' pin feathers emerged at a lower body mass, indicating a trade-off between allocating protein toward pin development instead of body mass. Treatment tail feathers also grew around 2mm longer than controls. For some regions of the body, treatment nestlings developed pin tracks and pins earlier than controls, although the effect of light pollution does not seem to be driving this pattern of development. Different speeds of feather development in each body region are consistent with the observations of Fernaz et al. 2012.

Despite visual observations, we found no indication of wing or tarsus asymmetry from our models. Wing asymmetry can occur from incubation behavior where the mother did not roll the egg enough for even incubation on all sides (Clatterbuck et al. 2017). This has previously

been recorded in laboratory settings (Swaddle & Witter 1994; Coslovsky & Richner 2011) and is thought to be caused by energetic stressors (Swaddle & Witter 1994; Coslovsky & Richner 2011). Perhaps the asymmetry observations were caused by inexperienced mothers affected by stress or some other parental variable that was not measured in this experiment.

Sub-lethal effects are not easy to observe particularly when mitigated by physiological tradeoffs. Our findings suggest that ALAN is a stressor that prevents nestlings from maximizing growth of all traits. ALAN appears to cause nestlings to allocate resources to feather growth and metabolic maintenance at the expense of body mass and morphological development. Our findings have the biggest implications for urban ecology. Studies of urban birds show what I dub an “urban phenotype” – urban nestlings end up skinner and have shorter tarsi than rural counterparts (Caizergues et al. 2021), but with no difference in body condition (Bókony et al. 2012; Caizergues et al. 2021). But these studies are urban-rural comparisons that do not test underlying mechanisms. Our findings suggest that ALAN might account for some of the urban phenotype.

Further research is needed to tease apart confounding variables and better understand the effects of ALAN on nestling health and development. First, nestling growth and success are highly dependent on parental behavior, particularly provisioning rates. Future studies should also factor in adult nighttime restlessness, onset of foraging activity, and / or foraging period as a compounding effect on nestling development. Food intake, blood glucose, and body condition are all interconnected, so parental behavioral change has the potential to cause or mitigate sublethal effects in nestlings.

Second, it would also be useful to try this experiment with different wavelengths, intensities, and durations of artificial light. Previous studies have found differences in adult

behavior depending on the intensity and color spectrum of light. For example, blue colored lights (shorter wavelengths) are found to be more impactful on behavioral responses than red- or yellow-colored lights (longer wavelengths); although, all light colors do have some negative effect (Ouyang et al. 2015; Longcore et al. 2018). Soler et al. (2014) found that chicks that spent more time begging gained less mass and had lower immune response. ALAN could be a source of nestling restlessness, explaining why we observed lower mass in treatment chicks. Birds' onset of activity also began earlier at higher light intensities and lasted longer into the night (Dominonni et al. 2014; Stracey et al. 2014; De Jong et al. 2016). Short-term removal of ALAN ceased all negative behavioral effects, especially on migration (Van Doren et al. 2017), indicating that shorter nighttime durations of ALAN may help mitigate sublethal effects.

Finally, although we found no evidence that ALAN poses a risk of metabolic disease, future research should examine the possibility of immunosuppression and production of corticosterone. Producing corticosterone requires absorption of blood glucose, so metabolic disturbance or immunosuppression may have been happening, but went undetected in this experiment. Getting a direct measure of stress will help clarify the relationship between glucose, mass, and keratin by quantifying each sublethal effect in relationship to ALAN and each other. Stress-induced trade-offs during the nestling stage may have carryover effects into adulthood, potentially affecting age of first reproduction, first clutch size, and breeding frequency (Cooper & Voss 2013). If nestlings invest more energy in feather production at the expense of their body mass during the critical growth period, they may delay reaching sexual maturity or produce smaller clutches. For example, birds that experienced reduced body mass during development might have compromised physical condition as adults, affecting their foraging efficiency, migration success, and overall survival during challenging periods. These stress-induced trade-

offs could potentially have heritable, population-level consequences as well (Helm & Visser 2010). For example, if many nestlings in a population experience similar trade-offs, there may be reduced reproductive output, leading to lower population growth rates. In the most extreme cases, this could result in population decline or possibly local extinctions. However, over long periods of time, if stress-induced trade-offs persist across multiple generations, natural selection may favor individuals with genetic predispositions for better stress resilience and trade-off management (Helm & Visser 2010). This could lead to the evolution of traits that better balance the investment of resources between body growth and feather production, potentially mitigating the negative effects observed in the short term.

Like this experiment, most studies of ALAN involved low levels of illuminance (1-2 lux), which highlights the sensitivity of physiological systems to artificial light as well as the extreme challenge of mitigation efforts (Sanders et al. 2021). Urbanization is projected to increase every year with 68% of the world's population expected to live in cities by 2050 (United Nations 2019). Based on recent trends and projects in Kyba et al. (2023), the reach and intensity of ALAN will increase by 9.6% every year, making artificial light studies just as important as habitat loss and climate change in the realm of avian conservation. Studies like these explore the possibility of urbanization influencing a phenotypic shift in barn swallows and other aerial insectivores. We need to identify and quantify the consequences of this urban phenotype and figure out how to mitigate those consequences (see Chapter 3 for in-depth discussion).

V. Tables

Table 2.1: Developmental threshold score options for each body region in standardized nestling photos

Threshold Score	Score Meaning
‘Abs’ = Absent	No feathers, pins, or subdermal tracks can be seen on the nestlings. Nestling is “naked” with only down feathers.
‘Sub’ = Subdermal	Subdermal pin tracks can be seen on the nestling. No pins have emerged from the skin.
‘Em’ = Emerging Pins	Pins have broken through the skin, but no feathers have emerged from the pins.
‘Fp’ = Pin Feathers	Feathers are emerging out of the pins. Down feathers are molting.
‘Fcf’ = Full Contour Feathers	Feathers are long enough to cover pins. Nestling is beginning to have an adult-like appearance.

Table 2.2: Nest statistics for sample size, incubation, average clutch and brood, brood success, and predation. Stats show no difference between control and treatment nests.

Treatment	Number of Nest Attempts	Number of Nestlings	Avg. Clutch Size	Avg. Brood Size	Avg. Incubation Period (days)	% Eggs Hatched	% Chicks Fledged	Number of Predation Events
Control	32	101	4.15	3.73	18.0	65.0	81.0	13
Light Treatment	16	58	4.67	4.06	15.4	81.1	57.2	13
Standard Error	NA	NA	0.51	0.43	1.31	0.16	0.13	NA
P-value	NA	NA	0.32	0.44	0.08	0.34	0.08	NA

Table 2.3: Variable loadings from Principal Components Analysis showing the degree to which each variable contributes to the variations within each component.

Variable	Component 1 (Feathers)	Component 2 (Morphology)
Primary 1	-0.40	0.13
Primary 5	-0.40	0.13
Primary 9	-0.41	0.07
Head feather	-0.38	0.24
Tail feather	-0.29	-0.14
Right wing	0.04	0.42
Bill	0.13	0.51
Head	0.14	0.46
Right tarsus	0.17	0.45
Left wing	0.31	0.04
Left tarsus	0.34	-0.17

Table 2.4: Component 1 linear mixed model results. Component 1 is composed of primary 1, primary 5, primary 9, and head feather. No difference between treatment and control.

Variable	β	SE	t-value	p-value
Intercept	-5.36	0.38	-14.11	0.0000*
Age	0.73	0.03	21.36	0.0000*
Light Treatment	0.87	0.52	1.65	0.10

Table 2.5: Component 2 linear mixed model results. Component 2 is composed of head, bill, right wing, and right tarsus length measurement. Treatment nestlings developed slower than controls.

Variable	β	SE	t-value	p-value
Intercept	-3.62	0.18	-19.89	0.0000*
Age	0.52	0.01	36.46	0.0000*
Light Treatment	-0.55	0.26	-2.12	0.03*

Table 2.6: Mass model results showing treatment nestlings weighing around 1 gram lighter than controls.

Variable	β (g)	SE	t-value	p-value
Intercept	0.89	0.28	3.16	0.002*
Age	1.35	0.02	60.84	0.0000*
Light Treatment	-1.02	0.40	-2.55	0.01*

Table 2.7: Tail feather length model results showing treatment nestlings growing longer tail feathers by about 2mm.

Variable	β (mm)	SE	t-value	p-value
Intercept	-1.27	0.36	-3.54	5e-04*
Age	0.27	0.02	11.40	0.00*
Light Treatment	2.12	0.50	4.28	0.00*

Table 2.8: ‘Sub’ photo scoring age and mass model results. There is no difference between treatment and control nestlings. The thigh body region develops faster.

Variable	Age Model				Mass Model			
	β (days)	SE	t-value	p-value	β (g)	SE	t-value	p-value
Intercept (back, control)	3.76	0.32	11.58	0.0000*	4.86	0.47	10.38	0.0000*
Light Treatment	0.82	0.59	1.40	0.18	0.48	0.86	0.56	0.58
head-nape	-0.25	0.18	-1.41	0.16	-0.32	0.26	-1.23	0.22
wings	0.13	0.11	1.23	0.22	-0.25	0.27	-0.94	0.35
thigh	0.36	0.18	1.97	0.05*	0.60	0.26	2.27	0.02*
tail	-0.05	0.18	-0.26	0.80	-0.09	0.26	-0.34	0.73

Table 2.9: ‘Em’ photo scoring age and mass model results. Treatment nestlings emerge pins at 2.5g lighter than controls. The thigh body region also develops faster.

Variable	Age Model				Mass Model			
	β (days)	SE	t-value	p-value	β (g)	SE	t-value	p-value
Intercept (back, control)	8.09	0.57	14.32	0.0000*	12.67	0.62	20.55	0.0000*
Light Treatment	-0.84	1.04	-0.80	0.43	-2.52	1.13	-2.23	0.04*
head- nape	0.43	0.23	1.89	0.06	1.16	0.46	2.49	0.01*
wings	-0.03	0.21	-0.13	0.90	-0.16	0.44	-0.36	0.72
thigh	0.63	0.23	2.78	0.006*	1.74	0.47	3.73	0.0002*
tail	0.04	0.23	0.16	0.87	0.09	0.47	0.19	0.85

Table 2.10: ‘Fp’ Photo scoring age and mass model results. There is no difference between treatment and control nestlings. The thigh body region develops faster.

Variable	Age Model				Mass Model			
	β (days)	SE	t-value	p-value	β (g)	SE	t-value	p-value
Intercept (back, control)	11.12	0.64	17.48	0.0000*	17.59	0.45	39.09	0.0000*
Light Treatment	-0.78	1.47	-0.53	0.60	-1.54	1.06	-1.46	0.17
head- nape	-0.04	0.22	-0.17	0.87	0.04	0.20	0.18	0.86
wings	0.08	0.19	0.43	0.67	0.11	0.18	0.59	0.56
thigh	-0.05	0.41	-0.13	0.90	0.02	0.39	0.06	0.95
tail	0.19	0.19	0.96	0.34	0.20	0.18	1.09	0.28

Table 2.11: BCI with tarsus and wing model results. Both models show no difference in body condition between treatment and control.

Variable	BCI Tarsus Model				BCI Wing Model			
	β (mm)	SE	t-value	p-value	β (mm)	SE	t-value	p-value
Intercept	-0.18	0.02	-7.55	0.0000*	-0.04	0.02	-1.86	0.06
Age	0.03	0.002	16.36	0.0000*	0.002	0.001	2.37	0.02*
Light Treatment	-0.01	0.03	-0.30	0.76	0.02	0.03	0.91	0.37

Table 2.12: Physiology model results. Neither fat score nor blood glucose levels differed between treatment and control

Variable	Fat Score Model				Blood Glucose Model			
	β	SE	t-value	p-value	β (dg/mL)	SE	t-value	p-value
Intercept	-0.05	0.02	-2.43	0.02*	251.06	7.63	32.91	0.0000*
Age	0.02	0.002	7.79	0.0000*	1.11	0.36	3.10	0.002*
Light Treatment	-0.001	0.03	-0.04	0.97	14.92	10.69	1.40	0.17

Table 2.13: Asymmetry with wing and tarsus model results. Both models show no difference in between treatment and control.

Variable	Wing Asymmetry Model				Tarsus Asymmetry Model			
	β (mm)	SE	t-value	p-value	β (mm)	SE	t-value	p-value
Intercept	0.01	0.62	0.02	0.99	-0.07	0.10	-0.65	0.52
Age	0.16	0.05	3.08	0.0024*	0.01	0.01	0.76	0.45
Light Treatment	-0.55	0.75	-0.73	0.47	0.12	0.12	0.96	0.35

VI. Figures

Figure 2.1: Example of a standardized growth photo showing the chick on its stomach, Nestling ID, date, and a ruler.

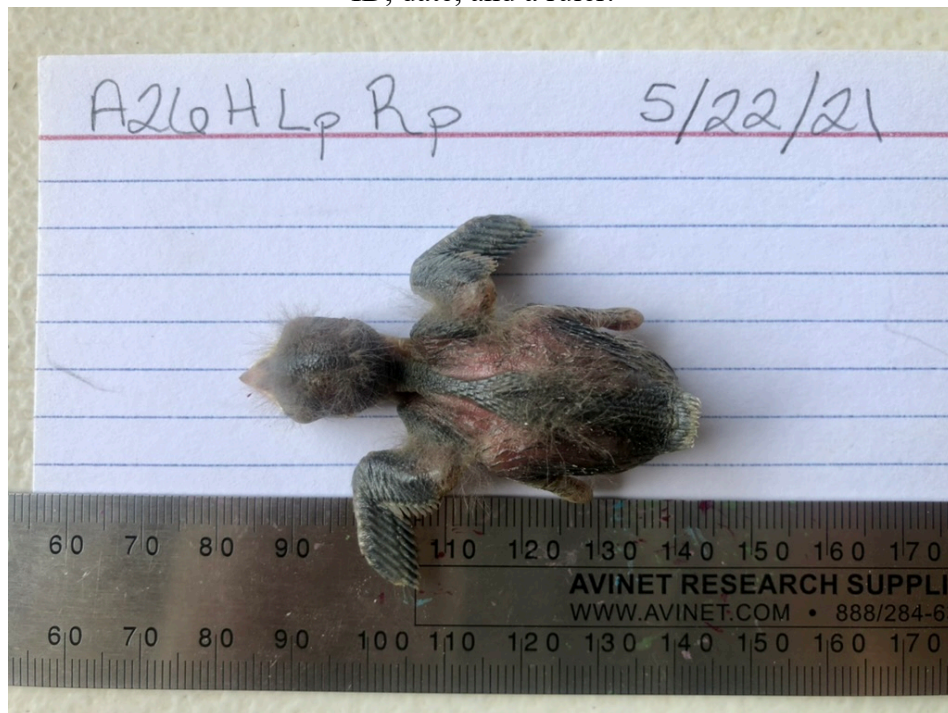


Figure 2.2: Photo of an ALAN nestling with extreme wing asymmetry. Other cases of asymmetry were visually noticeable, but less severe.



Figure 2.3: PCA analysis biplot graph showing correlation of all variables. Except for tailfeather, all feathers cluster together with the highest correlations to form Component 1. With the exceptions of leftwing and lefttarsus (presumably due to lack of data), all morphological measurements cluster together with the 2nd highest correlations to form Component 2.

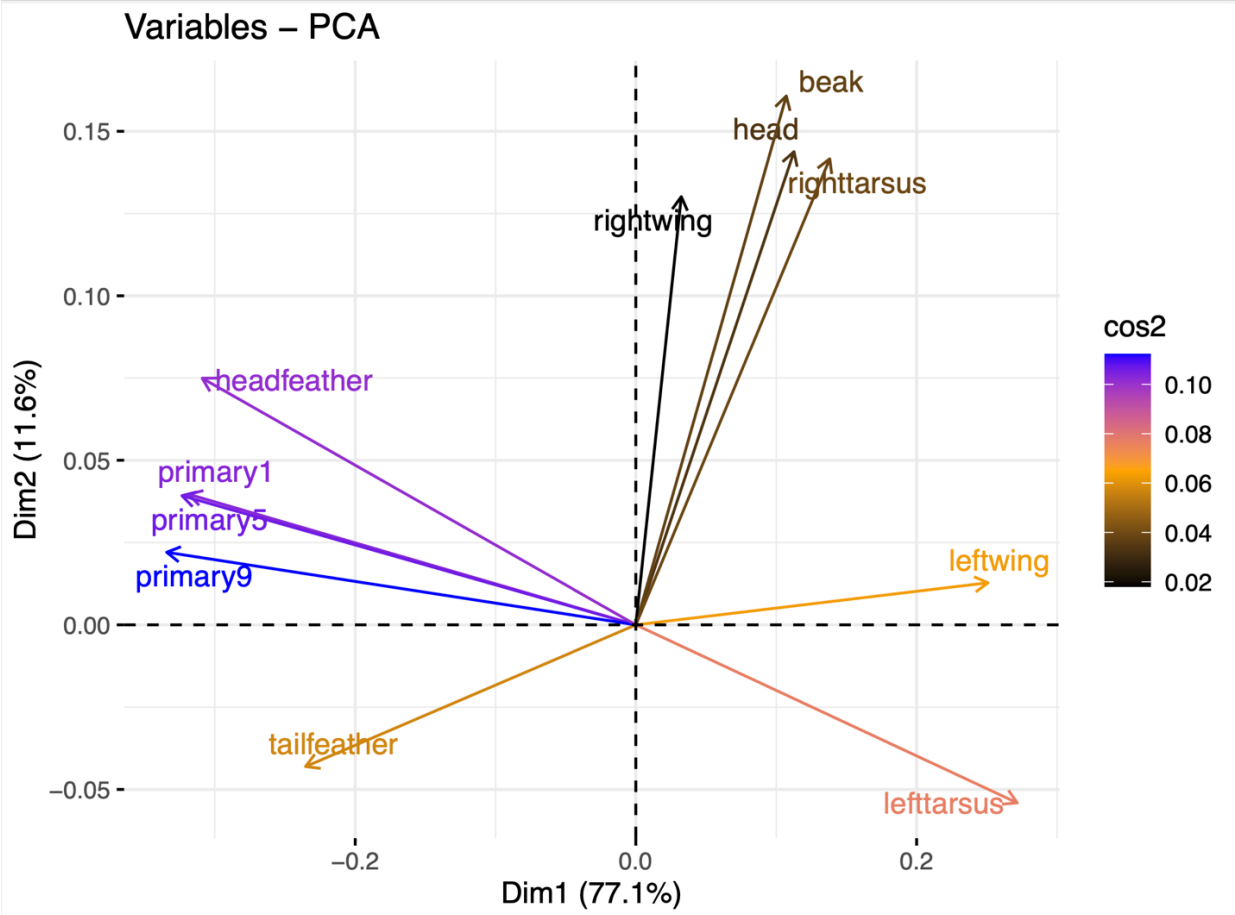


Figure 2.4: A scree plot from the PCA analysis showing which components make up the percentage of explained variances within the dataset. Component 1 (feathers) makes up 77.1%, while Component 2 (morphology) makes up 11.6%.

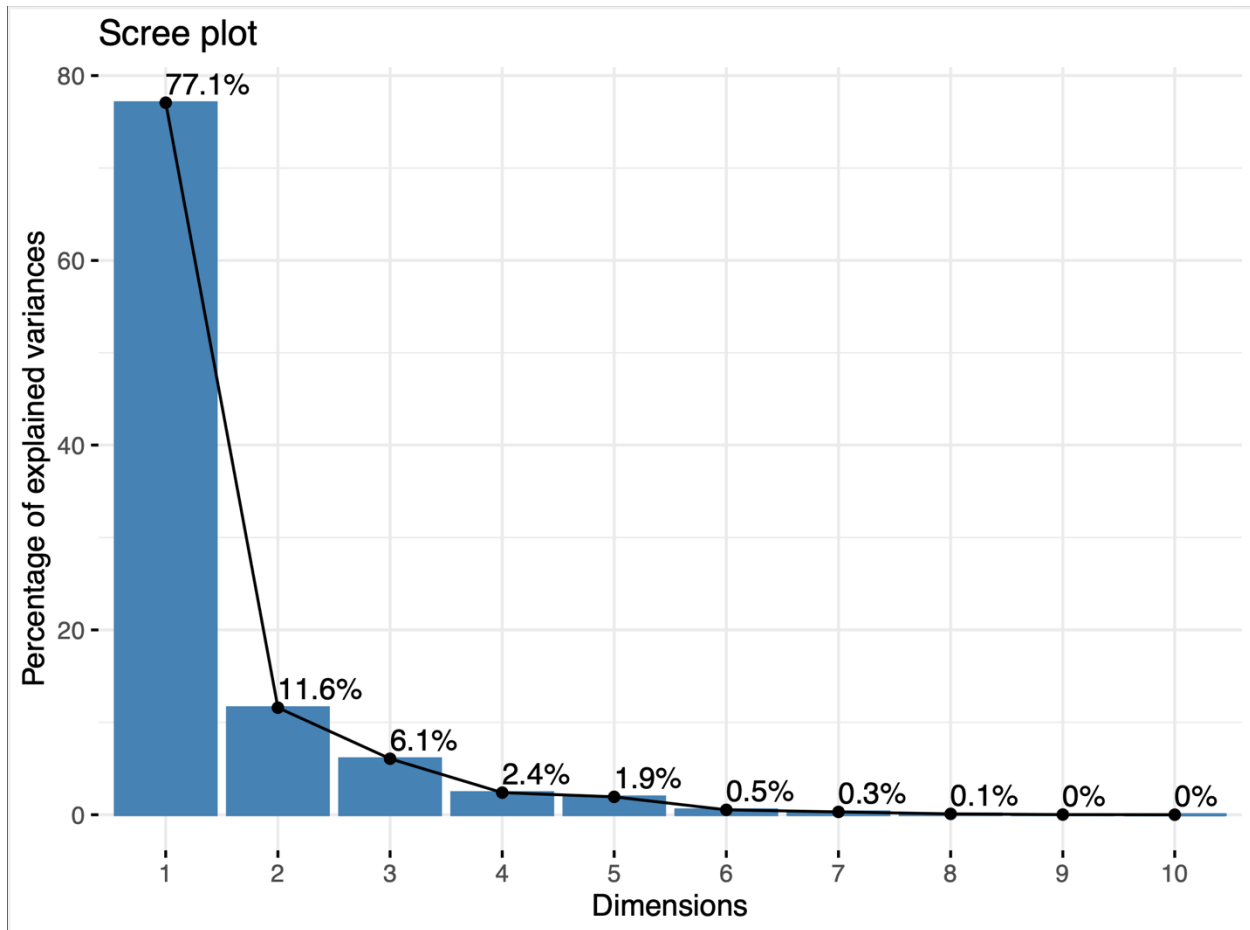


Figure 2.5: BARS nestling mass graph using predicted mass values. Shows control nestlings have heavier average mass than treatment nestlings.

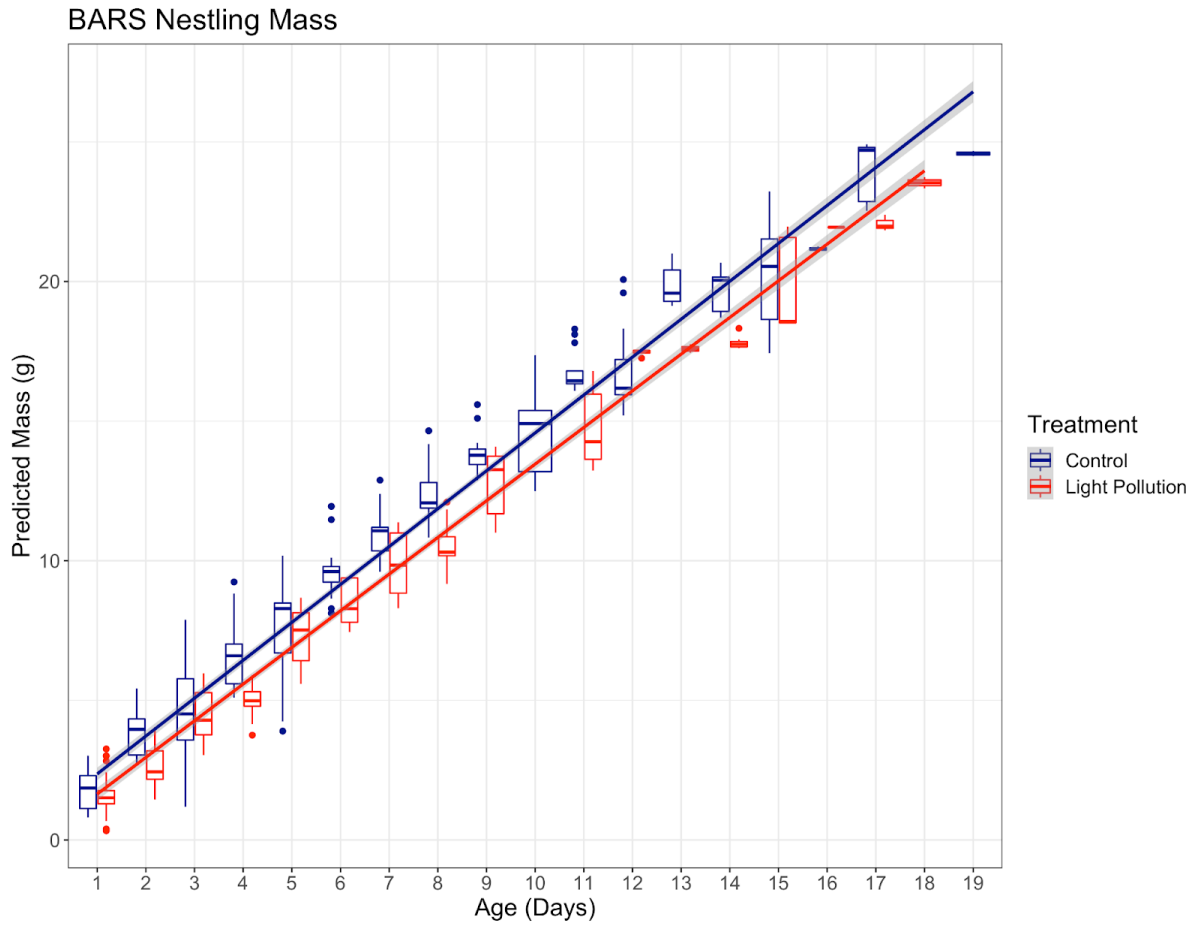


Figure 2.6: BARS Nestling Tail Feather Length: Shows treatment chicks have longer tail feathers than control.

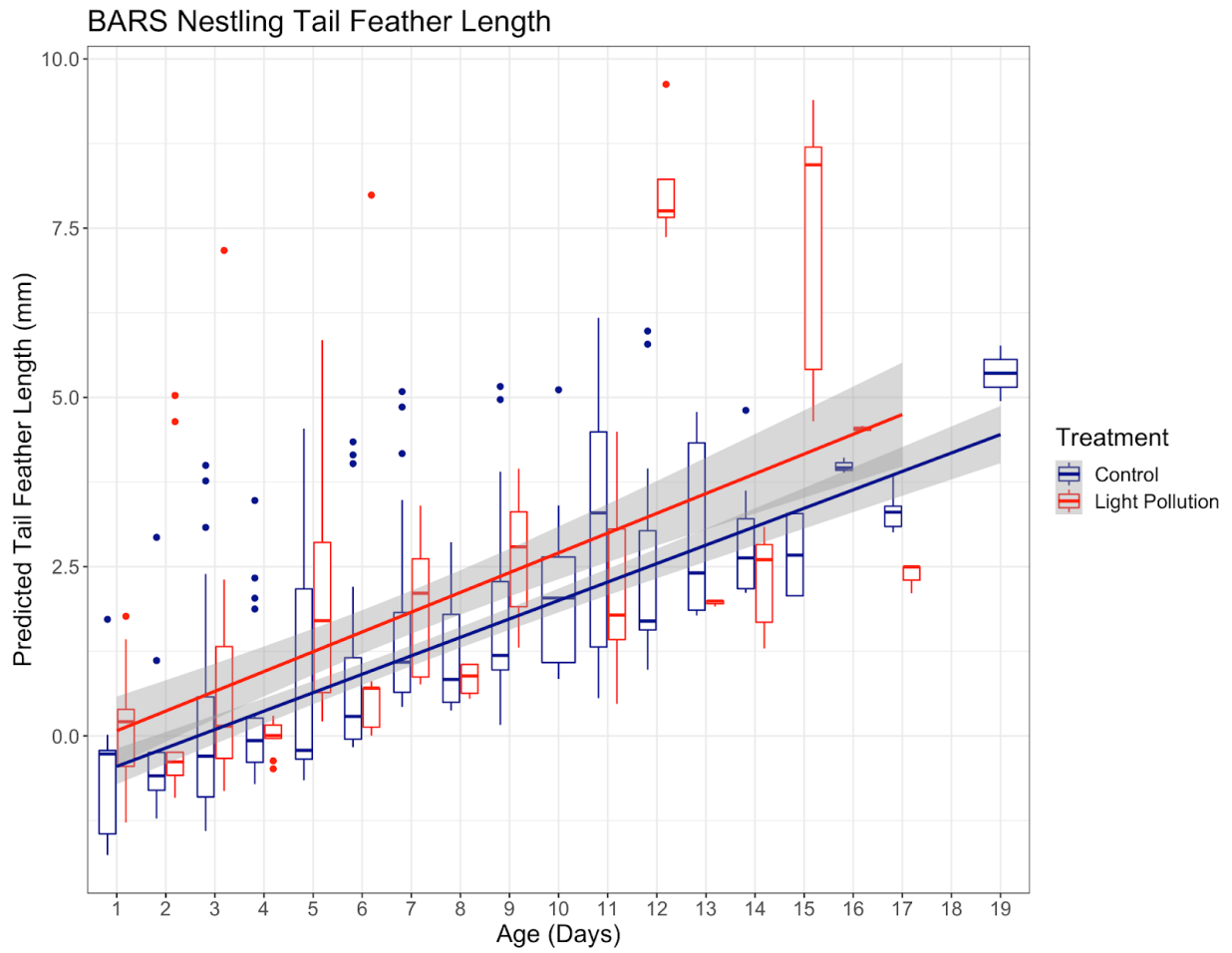
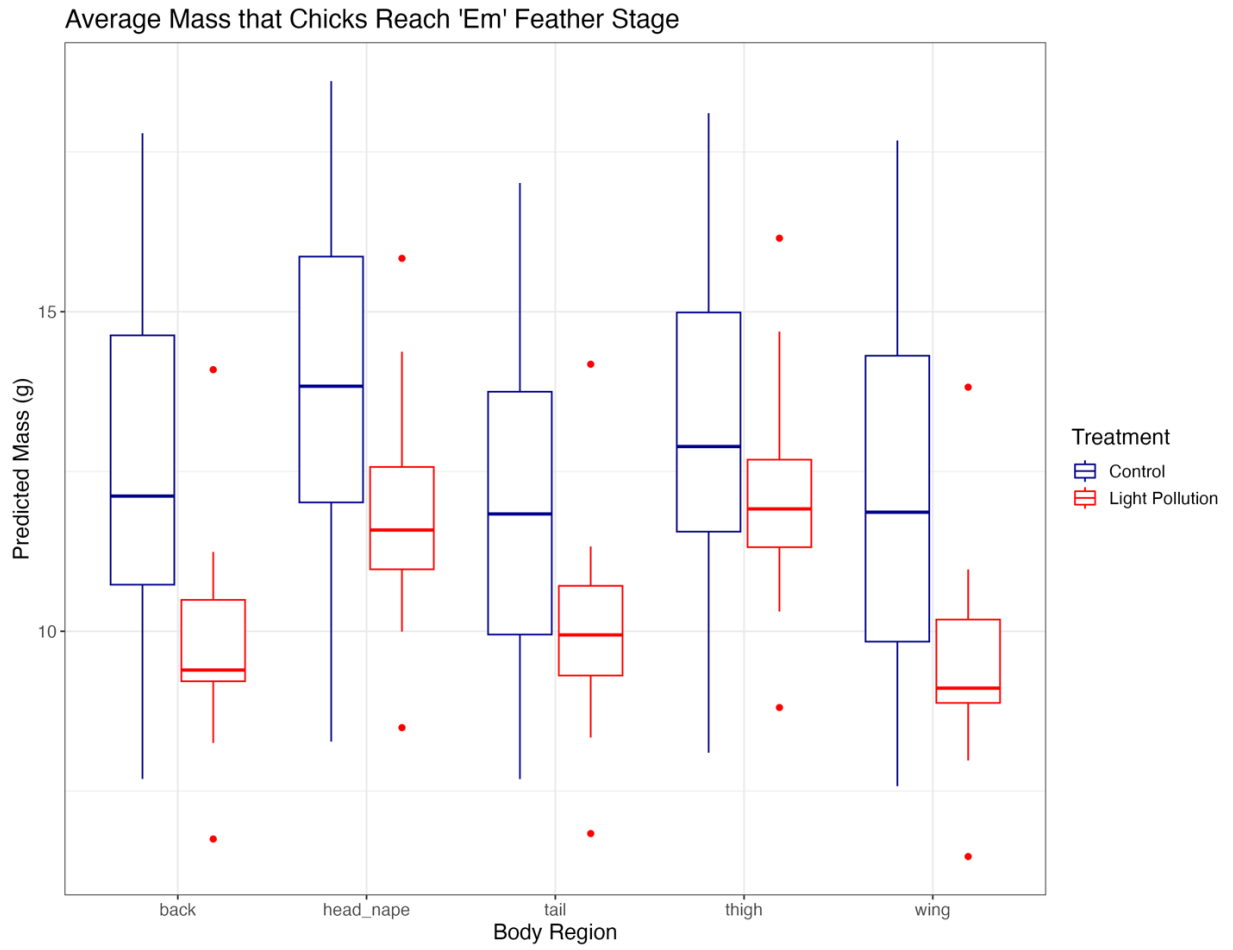


Figure 2.7: Em-Mass Graph: Shows that control chicks reach emerging pins stage at heavier masses than treatment chicks.



VII. Supplementary Material: Half Night Preliminary Data

To investigate the usefulness of curfew lighting, we ran an analysis using a portion of data from our field experiment exposing Barn Swallow nestlings to ALAN (see Ch. 2 for full experimental setup details). In 2021, we attempted to employ a half night treatment in which nestlings experienced a curfew - ALAN for the first half of the night and natural darkness for the second half of the night. Due to predation issues, we discontinued this treatment in favor of increasing full night sample size. This preliminary analysis might help give insight to the physiological effects of an ALAN curfew.

Our sample size for the half night treatment is 118 observations of 22 chicks in 6 nests. We used linear mixed models with random effects of Nest ID and repeated measures of Chick ID with age as a covariate. Although half night treatment was only used in 2021, we included full night treatments from 2020-2022; we checked to see if variables were affected by year, and they are not ($b = 0.70 \pm 0.37$, $t = 1.90$, $p = 0.08$).

We found that mass ($b = 2.15 \pm 0.46$, $t = 4.66$, $p = 0.0000$, Figure S1), wing length ($b = 4.52 \pm 1.44$, $t = 3.14$, $p = 0.003$, Figure S2), and bill length ($b = -0.90 \pm 0.25$, $t = -3.56$, $p = 0.0007$, Figure S3) differed between treatments. Half night treatment chicks were heavier than full night chicks by about 2 g. Half night wings were on average 4.5mm longer than full night. However, bill lengths in the half night treatment were almost 1 mm shorter. Tarsus length, fat, glucose, and primary feathers did not differ between half and full night.

We estimated a body condition index (BCI) using residuals from an ordinary least squares model using mass and wing length. We analyzed these residuals using a linear mixed model with random effects of Nest ID and repeated measures of Chick ID with age as a

covariate. The body condition of nestlings in half treatment did not differ from nestlings in full treatment ($b = 0.05 = 4 \pm 0.03$, $t = 1.41$, $p = 0.16$).

Half night nestlings having a heavier mass indicates more protein is allocated to building skeletal muscle than full night nestlings, perhaps because chicks are less stressed or at least not constantly stressed and have time to rest. We see a similar allocation to skeletal growth, due to half night nestlings' longer wings chords. Shorter bills in half night suggests less keratin production, which may indicate a potential trade-off in protein allocation to mass (skeletal muscle) over the bill (keratin production). These preliminary findings suggest that curfew lighting might mitigate some of the harmful sublethal effects of ALAN and are worth exploring in future research.

Figure S1: BARS nestling mass between curfew and full night nestlings, showing that curfew nestlings had a higher average mass.

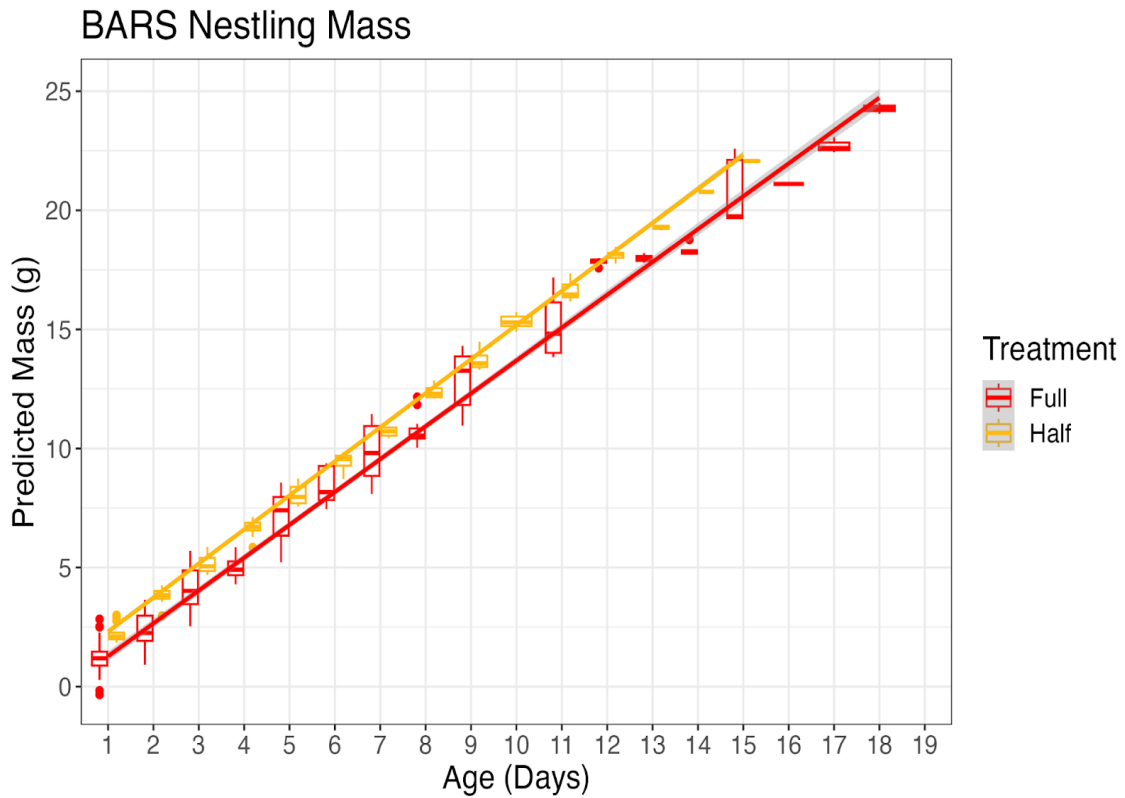


Figure S2: BARS nestling wing chord length between curfew and full night nestlings, showing that curfew nestlings had longer wings.

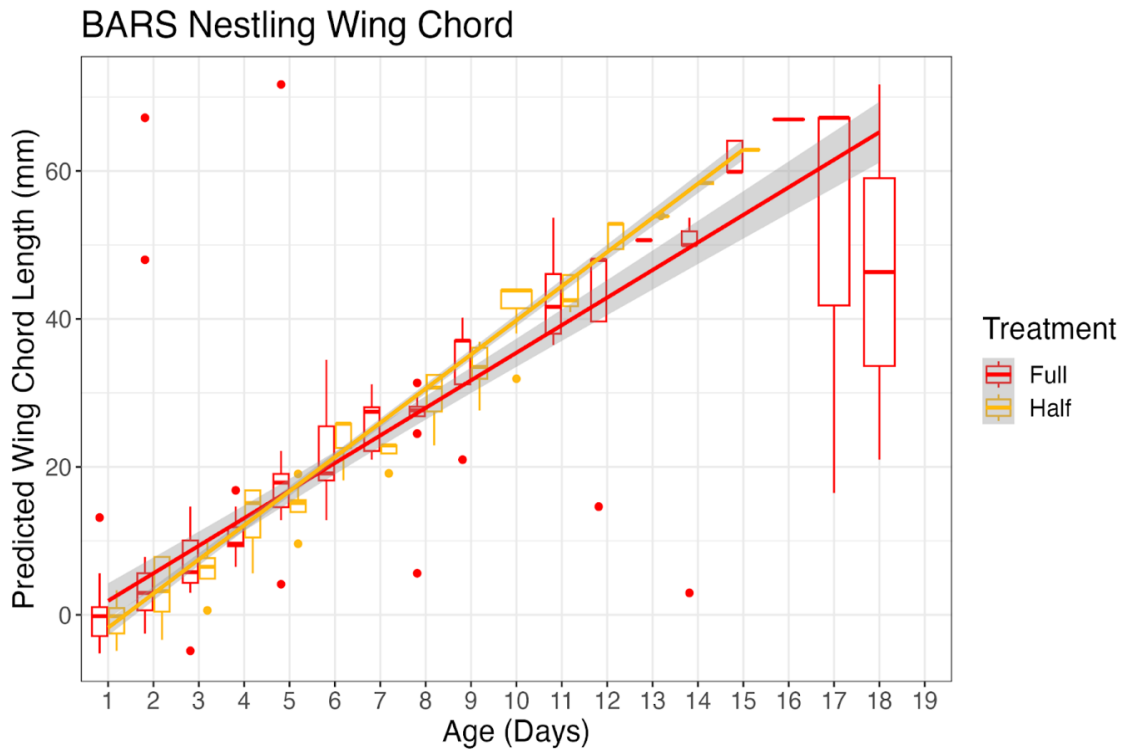


Figure S3: BARS nestling bill length length between curfew and full night nestlings, showing that curfew nestlings had shorter bills.

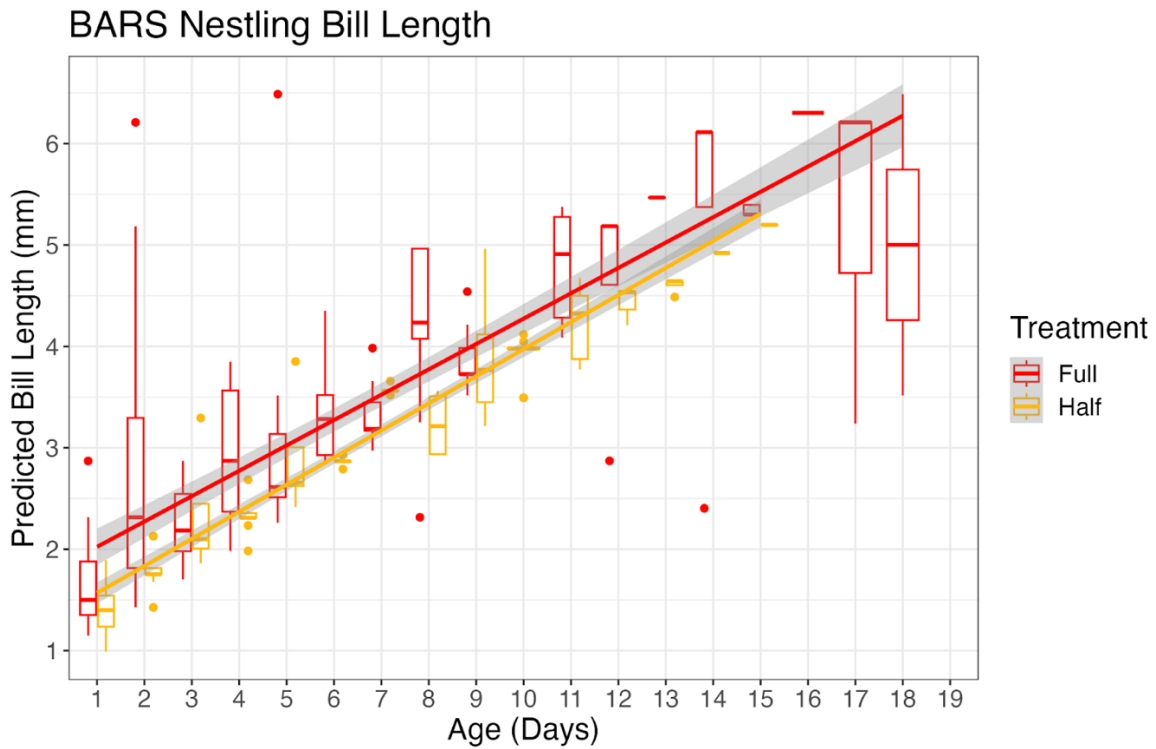
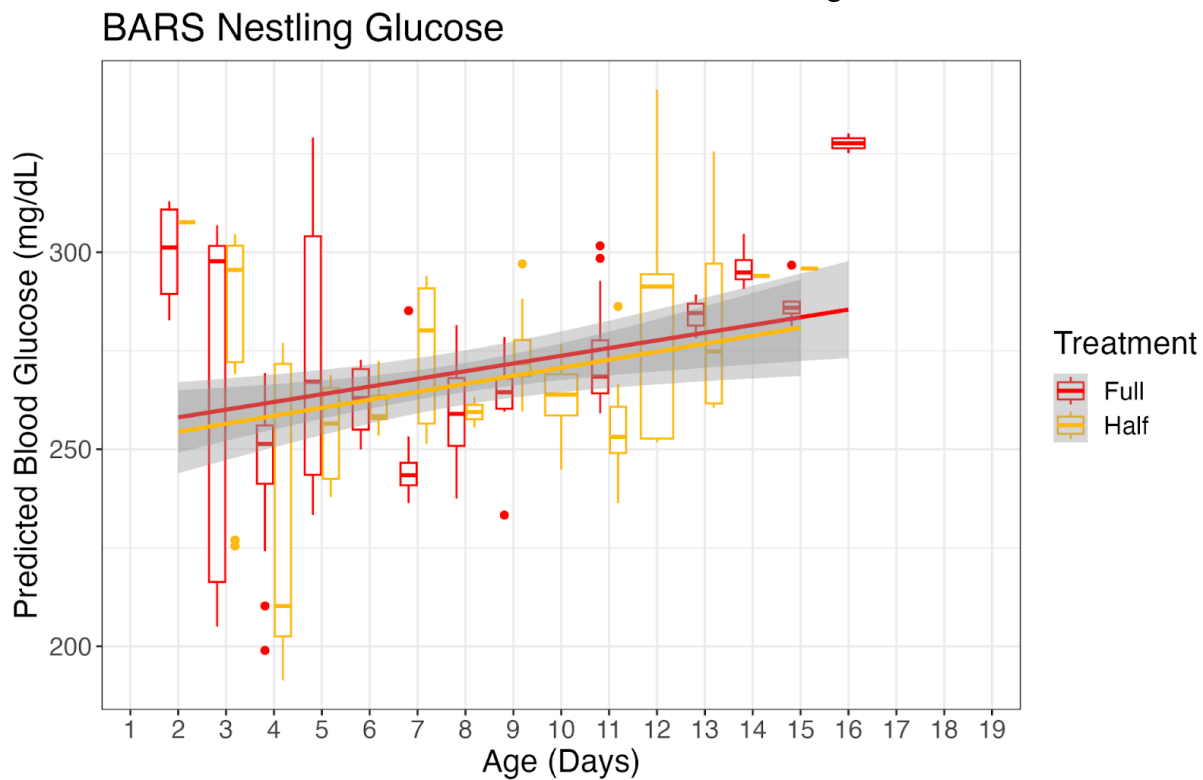


Figure S4: BARS nestling blood glucose between curfew and full night nestlings, showing no difference between curfew and full night.



CHAPTER 3: What to do about ALAN? Potential Solutions from Insights on Avian Physiological Mechanisms

I. ALAN as a Novel Environmental

Artificial light at night (ALAN) is characterized by the over-illumination of the night sky by artificial lighting. ALAN comes from the artificial lights on billboards, streetlamps, houses, office buildings, and other lit public areas of urban environments (Newport et al. 2014; Ouyang et al. 2015). However, ALAN is not contained to only cities, because light trespass and skyglow can project beyond urban environments. Light reflects off surfaces, creating skyglow beyond urban environments (i.e., trespass). ALAN is a form of anthropogenic change that is a prevalent component of nightscapes worldwide and causes pervasive ALAN across all ecosystems on Earth. Citizen science reports an immense reduction of visible stars from 2011 to 2022 (Kyba et al. 2023). Growth in human population and infrastructure has been accompanied by exponential increases in artificial night lighting (Francis and Barber 2013; Longcore and Rich 2004). The projected rate of increased skyglow is anywhere from 2-10% per year, depending on method of measurement (Kyba et al. 2023). If this is how our world is lit, we must continue to analyze the consequences of ALAN on the environment.

ALAN is an environmental pollutant (Falchi et al. 2023; Kyba et al. 2023). Population-level conservation issues related to ALAN, such as window collisions (Longcore & Rich 2004; Newport et al. 2014; Van Doren et al. 2017) and changes in migration and orientation (Longcore & Rich 2004; Helm et al. 2013; Van Doren et al. 2017), have been well-studied. Laboratory and site-specific studies (summarized in subsequent sections) have demonstrated that artificial night lighting can cause novel harm to wildlife behavior and physiology. Different behavior and physiological effects in urban birds compared to non-urban birds could be characterized as an

“urban phenotype.” An ALAN-induced behavioral urban phenotype might include birds in urban environments advancing morning onset of activities such as foraging (Dominoni et al. 2013b; Raap et al. 2015; De Jong et al. 2016; Dominoni et al. 2022) or dawn song (Kempnaers et al. 2010; Da Silva et al. 2015; Derryberry 2017), extending foraging later into the night (Longcore & Rich 2004; Newport et al. 2014; Russ et al. 2015; De Jong et al. 2016), and engaging in more extra-pair copulations (Kempnaers et al. 2010; McNaughton et al. 2021). Meanwhile, the physiological markers of an urban phenotype might include lower body mass (Braun & Sweazea 2008; Lill 2011; Kaliński et al. 2014; Swaddle et al. 2015) or body condition (Ouyang et al. 2015; Lamb et al. 2016), and increased markers of metabolic stress (Ouyang et al. 2015; De Jong et al. 2016; Lamb et al. 2016). Chapter 2 explains some of these physiological markers in depth and provides experimental evidence of barn swallows showing trade-offs between body mass, keratin production, and skeletal growth.

For many avian species, particularly songbirds, this urban phenotype is hypothesized to have negative consequences to fitness. Birds have experienced lethal and sublethal effects (which are summarized in our literature synthesis) due to ALAN. Understanding how birds compensate for disruptions of artificial light at night, and whether potential lighting alternatives mitigate sublethal effects, will provide insights into the limits to which birds can adjust to anthropogenic changes. In this paper, we synthesize many of the studies that explore the mechanisms of the photoperiod-fitness relationship and the consequences of ALAN impacting that relationship.

II. ALAN as a Selection Pressure and Shaper of Life History

In general, a trade-off describes an increase in fitness of one trait at the cost of a detriment to fitness in another trait. This system plays an important role in the life history strategies of many organisms, usually between survival and reproduction (Raap et al. 2016). Trade-offs occur due to limited resource availability; otherwise, natural selection would push all traits related to fitness to max capacity (Stearns 1989), which is not biologically possible. Many environmental forces can structure a trade-off including food availability, climate, temperature, and photoperiod. Tradeoffs are a key assumption and explanation of optimality models of life history evolution (Clutton-Brock et al. 1982, Stearns 1989). Physiologically, life-history trade-offs result from competitions among internal functions for limited internal resources, which results in differential allocation of the limited resources to one function instead of another, as represented in the “Y” model of resource allocation (Van Noordwijk & De Jong 1986; De Jong 1993). Other classic trade-offs in avian life history studies include between reproduction and immunocompetence (Sheldon & Verhulst 1996), and trade-offs involved in shaping the pace-of-life (e.g., metabolism and survival). When energy is limited, tradeoffs also occur at the cellular level. For example, a cell might allocate amino acids to make glucose or to make proteins.

When stress is introduced into the environment, new trade-offs might become apparent as organisms allocate resources to one internal function over another. Stress hormones have pleiotropic effects influencing gene transcription and consequently several traits simultaneously, mediating physiological tradeoffs (Lessells 2008). Rapid anthropogenic changes in night lighting alter evolutionarily stable sensory environments, making ALAN an environmental stressor. Stressful conditions can cause elevated corticosteroid levels in birds which increase gluconeogenesis and survival (Wingfield et al. 1998) while suppressing reproduction and

immune system (Wingfield et al. 1998; Raap et al. 2016). These competing energetic needs and constraints play a role in shaping avian life history trade-offs.

For nestlings, it is important to note that trade-off between growth rate of skeletal bones, which is maintained, and body mass and keratin production, which is reduced, might be inconsequential considering that nestling feathers are quickly molted, and bills continue growing throughout a bird's life (Van Hemert et al. 2012). In addition, any trade-offs made may not necessarily be detrimental to survival, especially when still receiving care and protection from adults. What we might observe is phenotypic plasticity caused by environmental forces during key points in development (Forsman 2015).

Because ALAN affects the entire ecosystem, it also likely has several indirect relationships on individual fitness. Studies find that ALAN advances the initiation of dawn song (De Jong et al. 2016; Kempenaers et al. 2010; McNaughton et al. 2021), which may be affecting sexual selection through perceived male fitness (Longcore & Rich 2004; Kempenaers et al. 2010; McNaughton et al. 2021) and increased extra-pair copulations (Kempenaers et al. 2010; McNaughton et al. 2021). Lower intensity lighting increased ground-dwelling insect activity, which relates to nestling food provisioning and nutrition (McNaughton et al. 2021). ALAN may indirectly impact native species fitness due to competition from invasive species (Ouyang et al. 2015; McNaughton et al. 2021; Sordello et al. 2022), which typically have greater behavioral plasticity and are more likely to be urban exploiters (McNaughton et al. 2021).

III. Physiological Responses to ALAN

Natural photoperiods consist of light and dark phases. Sunlight has shaped fundamental properties of biological organisms. Virtually every organism on Earth relies on sensory systems

to receive and respond to photoperiod cues of daily and seasonal cycles of light and dark (Foster et al. 2004; Dominoni et al. 2013a; Huffeldt 2020). Although sunlight provides illumination necessary for vision, sunlight also regulates essential non-image forming processes such as circadian timing systems, neuroendocrine rhythms, and acute alerting effects. These phases partition animal behavior into cycles of activity and rest. As such, photoperiod represents a strong selective force capable of shaping animal physiology. Changes in the duration or intensity of light or dark phases are thus likely to produce measurable changes in vertebrate circadian physiology (Cooper et al. 2009; Liu et al. 2022).

A. Systems that Detect Photoperiod

Clock genes control daily and annual life history (Gupta & Malik 2019). Clock genes are regulated by complex interactions between sensory input, the central nervous system, hypothalamus, pituitary glands, and various neuroendocrine and metabolic pathways (Gupta & Malik 2019; Dominoni et al. 2022). In birds, light penetrates not only through the eyes, but through complex systems involving regulation from the pineal gland, pituitary gland, and hypothalamus (Reinert & Wilson 1996; Gupta & Malik 2019; Wu et al. 2022). Photic input regulates clock genes through signaling secretion levels for various hormones. For example, light plays a huge role in determining melatonin secretions (Helm et al. 2013; Gaston et al. 2013; Wu et al. 2022). Daily melatonin rhythms are in turn regulated by the pineal gland (Cassone & Menaker 1984; De Jong et al. 2016; Gupta & Malik 2019; Wu et al. 2022). Thus, synchronization between light cycles and biological receptors are imperative to individual fitness.

B. Photoperiodic Timing Cues

The timing of light and dark phases is critical to biological health by synchronizing internal biological rhythms. In birds, the most reliable internal biological clock cue is photoperiod (Helm et al. 2013), or daily rate of change in photoperiod (see Ch. 1 results). Birds use circannual photoperiod to time life history events and phases, such as reproduction and gonadal development (Underwood et al. 2001; Kempnaers et al. 2010; Dominoni, Quetting, & Partecke 2013; Helm et al. 2013; Gupta & Malik 2019), molt (Gupta & Malik 2019), and migration (Gwinner 1986; Helm et al. 2013; Gupta & Malik 2019), each of which requires a host of neuroendocrine functions (Helm et al. 2013). Circadian photoperiod is also important for (and works in tandem with circannual rhythms) for many daily functions (Gupta & Malik 2019). For example, photoperiod is instrumental in determining clutch size, particularly the start and termination of egg laying (Kempnaers et al. 2010, see Chapter 1 (NestWatch) literature review).

C. Disruption of Circadian Rhythm and Subsequent Stress Responses

Disruptions to circadian rhythms and behaviors are proximate responses to a constant environmental stressor (Callow 1989). Birds have heritable circadian rhythms (Helm and Visser 2010) that align themselves with light–dark cycles, whereby natural light acts as a synchronizer (Zeitgeber) (Gwinner and Brandstätter 2001). ALAN is a novel selection pressure that alters photoperiodic timing cues. ALAN can impair sensory capabilities and create mismatches between cues and highly conserved physiological and behavioral responses, producing consequences that span behavior, ecology and evolution, and must be considered alongside other drivers of ecological patterns and phenomena (Longcore & Rich 2004; Swaddle et al. 2015;

Sordello et al. 2022). Here, we think about stress as a suite of physiological responses instead of a singular characteristic of the environment.

ALAN can directly cause stress. Studies in the poultry field have begun to experimentally address the effects of lighting regimes on egg production, egg mass, and growth for meat consumption (Molino et al. 2015; Wu et al. 2022). Poultry egg laying rates fluctuate with photoperiod length (Molino et al. 2015) and respond to ALAN between 5-20 lux (Molino et al. 2015; Wu et al. 2022), which is comparable to street lighting. Furthermore, developing domestic fowl exposed to experimental 24 hour photoperiods exhibit increases in body mass, larger than normal adrenal glands (the source of glucocorticoid hormones), elevated adrenal cholesterol production, and elevated blood lipid levels, indicating that they were stressed (Freeman et al 1980).

When confronted with stressors, vertebrates respond through two central systems, or “stress axes,” to restore physiological homeostasis (Palme et al. 2005). In birds, these hormonal axes are the sympatho-adrenal (SA) and the hypothalamic-pituitary-adrenocortical (HPA). Both the SA and HPA are regulated through adrenal glands that secrete catecholamine and glucocorticoid hormones (Palme et al, 2005). Cortisol and corticosterone are glucocorticoid hormones that stimulate energy mobilization, especially hepatic glucose release (i.e., the process of gluconeogenesis), to fuel the “fight or flight” response.

Corticosterone is the primary glucocorticoid hormone of birds. The physiological role of corticosterones are to mobilize energy stores in anticipation of activity. When a bird experiences stress, corticosterone secretion increases within a few minutes and can reach peak concentration in under an hour (Wingfield et al. 1998; Hau et al 2012). Studies find that stress raises corticosterone levels (Evans et al. 2012; Lamb et al. 2016; Injaian et al. 2018; Beaugeard et al.

2019), lower melatonin levels (Zivkovic et al. 2000; Raap et al. 2016; Sordello et al. 2022), and impaired immune function (Raap et al. 2016; Sordello et al. 2022).

Another direct physiological stress response is an increased demand for glucose. Stress causes the body to release glucose to ensure that there is enough energy prepared to fight or flee. Because flight is an energy-expensive action, birds naturally have a higher glucose level than mammals without any of the associated negative effects of high blood glucose (Beuchat & Chong 1998; Ardia 2006; Braun & Sweazea 2008). Parents need to increase their feeding rate to keep up with the physiological demand for glucose in stressed chicks (Ruiter et al. 2003; Downs et al. 2009). Even if the feeding rate does not increase, plasma glucose concentrations can remain high with a “spendthrift” phenotype as chicks convert glucose from other sources (Beuchat and Chong 1998). Chicks may convert glucose from any available lipids and proteins, which subsequently affects developing anatomy, such as the skeleton, feathers, or overall body mass (Ardia 2006; Downs et al. 2009; Kaliński et al. 2014). See Chapter 2 (Field Experiment) for an in-depth discussion of the role of glucose. Altricial songbirds mature in a matter of weeks, so a great deal of nutrients and energy is needed to sustain their growth. If ALAN creates an energy-deficit in nestlings, trade-offs in the form of reallocating available nutrients will have to occur in order to reach the fledgling stage.

ALAN may also cause indirect stress through the misalignment of circannual timing cues. For example, mismatches between migration to breeding grounds and seasonal food source availability may greatly affect reproductive success (Newport et al. 2014; Gupta & Malik 2019).

D. Cortisol Awakening Response

Physiological challenges from ALAN may occur due to a mechanistic analog of the Cortisol Awakening Response (CAR), a biological phenomenon understood predominantly from studies of both humans and mice. Under natural conditions, daylight triggers the cortisol awakening response (CAR), which involves the release of cortisol for about 30-45 minutes as vertebrates wake every morning (Clow et al. 2010; Thorn et al. 2004; Clow et al. 2010; Petrowski et al. 2019). CAR is crucial for the daily awakening process and preparing the body and mind for daytime activity while simultaneously reducing fatigue (Thorn et al. 2004; Clow et al. 2010). Cortisol released by CAR has been found to be completely independent of any other stress response that may occur throughout the rest of the day (Thorn et al. 2004; Clow et al. 2010). Healthy humans are able to unconsciously regulate how much cortisol is released by anticipating the stress load of the next day (Clow et al. 2010). For example, CAR measures are typically lower on the weekend when people do not have to go to work, thus anticipating less stress for the day (Clow et al. 2010).

CAR is sensitive to artificial light (Thorn et al. 2004; Clow et al. 2010; Petrowski et al. 2019), especially short wavelength light, aka blue light (Petrowski et al. 2019) or bright lights (Thorn et al. 2004; Petrowski et al. 2019). In humans, chronic stress, aging, clinical depression, slow wound healing, heart disease, and autoimmune disorders are all associated with constant cortisol signaling under artificial light (Clow et al. 2010). Under ALAN, the full sleep cycle is terminated because of the constant, light-based cue to be awake and active (Clow et al. 2010; Raap et al. 2015; Petrowski et al. 2019). When an organism interprets constant light as a stress signal (Ouyang et al. 2015), the CAR is continuously stimulated, releasing more cortisol than normal (Thorn et al. 2004; Petrowski et al. 2019).

A comparable glucocorticoid regulated mechanism similar to CAR is likely to exist in birds and other taxa as well. Under natural photoperiods, birds store unused nutrients, repair tissues, and recharge their bodies when they rest at night (Raap et al. 2015). We already see ALAN-induced symptoms in birds (summarized in Section 3c) that have been reported in mammals, disrupting these biological clock processes.

IV. Approaches to Mitigate Effects of ALAN

Architects design anthropogenic light at night with intensities and wavelengths to support human visual systems, public safety, and cost efficiency (Gaston et al. 2012; Barentine et al. 2020), but rarely consider other characteristics of light relevant to biological health. The problem of ALAN is a reversible global change. Regulation and governance of ALAN is typically to minimize nuisance light for astronomy observatories and dark sky parks and to minimize economic costs, but not typically related to human or wildlife health. The following approaches to outdoor lighting may help mitigate the lethal and sublethal effects of ALAN.

A. Light Intensity

Reducing light intensity could be effective in reducing skyglow as well as the negative physiological impacts experienced by birds. Horizontal light emissions (i.e., car lights, interior light escaping through uncovered windows, advertisement lighting, and unenclosed bulbs) produce the most skyglow (Gaston et al. 2012; Kyba et al. 2023) and often go undetected or under-detected by satellite measurements (Barentine et al. 2020; Kyba et al. 2023). Therefore, fixtures that enclose bulbs and contain emitted light downward will be beneficial in reducing light trespass and skyglow (Gaston et al. 2012; Kyba et al. 2023).

Reducing intensity increases melatonin secretion (Dominoni et al. 2013a; De Jong et al. 2016) and immune function (Raap et al. 2016), while reducing stress levels (Ouyang et al. 2015). However, all ALAN, even at its lowest intensity (< 1 lux), can still affect wildlife (Dominoni et al. 2013a; McNaughton et al. 2021). Birds may also perceive red light as less intense than other colors, even if lux is at the same intensity (Ouyang et al. 2015).

Over the past decade, outdoor lighting has replaced incandescent bulbs and high-pressure sodium lamps (HSPs) with light emitting diodes (LEDs). As of 2019, 47% of outdoor lighting are LEDs (Kyba et al. 2023). There's much debate if LEDs are effective in reducing light intensity and overall skyglow. Studies find that LEDs intensify skyglow and its ecological effects by scattering more blue light into the atmosphere (Falchi et al. 2016; Longcore et al. 2018; Barentine et al. 2020; Kyba et al. 2023). In the realm of ecology, LEDs are thought to be beneficial by reducing carbon emissions (Gaston et al. 2012) and providing increased foraging opportunity for some species (Longcore & Rich 2004; Longcore et al. 2018). Contrarily, in an experimental study in Tucson, AZ, Barentine et al. (2020) found that dimming LEDs from 90% to 30% of their full power draw only had a small reduction in local skyglow. However, dimmed lights may be more useful toward mitigating light trespass in natural landscapes (Gaston et al. 2012; Longcore et al. 2018; McNaughton et al. 2021). In addition, building collisions were reduced when periodically flickering lights were used instead of constantly burning lights (Gaston et al. 2012); similarly starlings had lower corticosterone levels in low-frequency, flickering light (Evans et al. 2012). Overall, LEDs produce limited ability to mitigate impacts to wildlife physiology, behavior, and survival (McNaughton et al. 2021).

B. Light Spectra

Widespread use of LEDs has shifted the outdoor lighting spectrum to shorter wavelengths (bluer light) (Gaston et al. 2012; McNaughton et al. 2021; Kyba et al. 2023). Blue light also scatters more strongly through the atmosphere than longer wavelengths (red and yellow light) of HSPs (Gaston et al. 2012; Barentine et al. 2020). Ecologically, blue light is the greatest reducer of melatonin (Gaston et al. 2012; Gaston et al. 2013) and induces high corticosterone levels (Ouyang et al. 2015). This is perhaps because birds perceive blue light as daytime (Yadav et al. 2015). Longer wavelengths have less ecological impact (Gaston et al. 2012; Longcore et al. 2018), particularly on foraging behavior (Gaston et al. 2012; Dominoni et al. 2013b; Russ et al. 2015), nighttime activity (Ouyang et al. 2017), and disease transmission (Ouyang et al. 2017). Ouyang et al. (2015) found no spectra effect on reproductive success; however, nests near long wavelengths of ALAN showed an increase in stress levels. Da Silva et al. (2017) found no relationship between light spectra and onset of dawn chorus. Keeping outdoor lighting to shorter wavelengths (red, yellow, amber) may cause less harm than blue or broad-spectrum white lights (Longcore et al. 2018; Falchi et al. 2023). Few studies on wild songbirds have been conducted on responses to different light spectra.

C. Light Curfew/ Duration

Street lights contribute around 20% of ALAN (Barentine et al. 2020). Contrary to popular belief, artificial lights can be turned off at night without affecting public safety (Kyba et al. 2017; Falchi et al. 2023). A large percentage of ALAN in cities is also from decorative and advertisement lighting (Kyba et al. 2023). Curfew lighting refers to the practice of turning off

street, security, and decorative lighting during a portion of the night. ALAN could be mitigated by turning off or dimming lights for periods during the night (Falchi et al. 2023), especially during important life history events such as migration and breeding; the hours before dusk and dawn are typically of most importance to many organisms (Gaston et al. 2012).

V. Future Research Directions

ALAN is not the only anthropogenic stressor that could be inducing an urban phenotype, but it is likely a significant one. Future research will have to explore how confounding factors, such as climate change and air pollution, interact with and potentially worsen the impacts of ALAN. Atmospheric conditions (e.g, cloudy versus clear skies) have an effect on the scattering of light particles (Longcore et al. 2018); the more particles in the sky, the more light scatters. Climate-driven changes in weather conditions, especially droughts and wildfires, exacerbate existing air pollution (Nolte et al. 2018), so may also cause areas already heavy in ALAN to appear even brighter. The interaction between climate change and photoperiod may also inform species range-shifts. Polar species are typically adapted to extreme photic conditions (e.g., months of continuous daylight). Thus, poleward range-shifts caused by climate change may be limited for organisms that can not readily adapt to longer photoperiods (Huffeldt 2020). Perhaps areas of intense ALAN could be comparable to areas of naturally longer photoperiod, giving an idea as to how local populations will respond to climate-induced photic changes. Experiments would compare light intensity and spectrum measurements, both visually and through satellite (Kyba et al. 2023), and atmospheric conditions from multiple of each type of environment. Areas that experience midnight sun may also have the benefit of being a zero visible stars “control”

environment to project potential physiological trade-offs and behavioral responses of reduced star visibility due to ALAN.

Another research question to explore is how different ALAN regimes (i.e., intensity, wavelength, duration) impact genotypic and phenotypic expressions. Phenotypes are adaptive to historic environmental conditions, in this case, natural photoperiods. Current phenotypes may be maladaptive given environmental change of pervasive artificial light at night. Activating Transcription Factor 4 (ATF4) is a protein encoded by the ATF4 gene. The ATF4 gene integrates stress signals in vertebrates, including birds (Johnston et al 2016). In mammals, upregulation of ATF4 impacts multiple pathways responsible for energy homeostasis, including glucose metabolism (Yoshizawa et al. 2009) and oxidative stress resistance (Harding et al 2003; Yoshizawa et al. 2009). Experimental expression of ATF4 may be key to understanding the genetic mechanisms producing tradeoffs among energetic and morphometric traits. For example, blood samples taken from birds in field experiments involving artificial lighting can be analyzed in the laboratory (e.g., qPCR analysis) to measure the levels of ATF4 expression. We would expect birds exposed to ALAN will have higher quantities of ATF4.

With urbanization occurring rapidly across the globe, it is important to examine urban effects and their implications for wild bird relationships with urban areas. There is a need for more experimental studies on wild birds (see Table 3.1 for research question summaries). Unlike other global change studies, we do not need to estimate effects based on projected future conditions, such as projected global mean temperatures. Instead, we mimic anthropogenic lighting options that occur now and that are competing approaches of lighting engineers. Understanding the relationship between types of artificial light and genotypic and phenotypic expression will help us determine the most promising future direction of outdoor lighting. These

types of experiments can provide an expected physiological - environmental feedback loop for particular species or populations over time. These experiments can also be particularly useful for management and conservation decisions. Researchers can provide evidence of the effects of ALAN on health and development and advocate for the implementation of dark infrastructures into conservation policy that reduce negative effects of ALAN. The outdoor lighting we choose as a society will ultimately dictate the avian urban phenotype.

Table 3.1: Summary of proposed future research questions categorized by study area.

Study Area	Research Topics
Population Responses	<ul style="list-style-type: none"> • Photoc environment limiting poleward range shifts • Measuring interactions between ALAN, atmospheric climate change, and air pollution
Organismal / Physiological Responses	<ul style="list-style-type: none"> • In depth blood analysis of glucose, proteins, and immune function in response to different ALAN regimes • Comparing urban phenotypes, particularly in areas of high ALAN, to phenotypes of species in northern latitudes with naturally longer photoperiods
Genetic Markers	<ul style="list-style-type: none"> • ATF4 gene analysis • Common garden or reciprocal transplant experiments with wild-caught nestlings from ALAN and northern latitudes to measure phenotypic vs genetic responses

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