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DIVERGENT RESPONSE TO ANTHROPOGENIC CHANGE WITHIN THE SONGBIRD TAXON: INSIGHTS FROM THE RANGE EXPANSION OF THE NORTHERN CARDINAL AND MITIGATION MECHANISMS FOR MIGRATORY BIRD-BUILDING COLLISIONS

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DIVERGENT RESPONSE TO ANTHROPOGENIC CHANGE WITHIN THE SONGBIRD TAXON: INSIGHTS FROM THE RANGE EXPANSION OF THE NORTHERN CARDINAL AND MITIGATION MECHANISMS FOR MIGRATORY BIRD-BUILDING COLLISIONS

By

Jenna Brewer

A THESIS

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MASTER OF SCIENCE

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This thesis has been approved in partial fulfillment of the requirements for the Degree of MASTER OF SCIENCE in Applied Ecology.

College of Forest Resources and Environmental Science

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Author Contribution Statement

Chapter 1 is a brief overview of the central connecting themes of this thesis. It aims to describe the broader objectives of the research and topics studied in the subsequent chapters.

Chapter 2 is intended to be submitted to peer-reviewed journal. Jared Wolfe, Kristin Brzeski and Jenna Brewer formulated the main idea and developed the study design. Samples were collected by Jared Wolfe, Erik Johnson, Daniel Baldassare and Jennifer Smith. Samples were prepared and measured for ptilochronology by Jenna Brewer. Samples were prepared for isotopic analysis by Jenna Brewer and final analysis was completed by Jennifer Eikenberry. Samples were prepared for corticosterone analysis by Jenna Brewer and final analysis was completed by Chris Tonra. Data was analyzed by Jenna Brewer and Jared Wolfe. Jenna Brewer wrote the original manuscript. Jared Wolfe contributed to manuscript structure and major edits. The final manuscript was edited and reviewed by David Flaspohler and Jill Olin.

Chapter 3 is a research report, the current extent of which is not intended for publication. Jared Wolfe, Zach Gayk and Jenna Brewer formulated the main idea and developed the study design. Shane Oberloier, Anders Smitterberg, Brandon Finley and Suhayb Zeqlam designed and assembled the speaker unit. Zach Gayk designed and engineered the acoustic sounds. Data collection was conducted by Jenna Brewer and Chicago Bird Collision Monitors. Data was analyzed by Jenna Brewer and Jared Wolfe. Jenna Brewer wrote the original manuscript. Jared Wolfe contributed to manuscript structure and major edits. The final manuscript was edited and reviewed by David Flaspohler and Jill Olin.

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Abstract

Anthropogenic activities have impacted ecosystems across the globe. However, wildlife species have exhibited heterogenous responses to these novel changes, with some species experiencing population growth, and others succumbing to population decline. I studied examples of both within the songbird taxon, focusing on drivers of range expansion in the Northern Cardinal and acoustic mitigation mechanisms for migratory bird-building collisions, a source of decline for many songbird species. I found that the Northern Cardinal’s range was primarily a function of climatic stress, which was supported by the modulation of the molt process across latitudes. Specifically, Northern Cardinals exhibited faster feather growth rates in colder climates, likely to avoid molting in adverse weather conditions. This has implications for drivers of population resilience, wherein wildlife species that exhibit life history plasticity may be imbued with greater global-change responsiveness. I also studied mortality mitigation strategies for songbird taxon experiencing population loss due to collisions with anthropogenic structures. I found that flight coordination of migratory birds could be manipulated through the projection of relevant acoustic signals. Specifically, I found that a playback of generalist songbird species acts as a migratory bird attractant and a 2-10 kHz broadband sound acts as a migratory bird deterrent, effectively directing birds away from unsafe airspace. This technology was employed at several large buildings in downtown Chicago to address high numbers of migratory bird collision mortalities. Both research projects address the nuanced manner in which anthropogenic influence has modified wildlife species population dynamics, providing insight into drivers of species resilience and new applied conservation methodologies.

1 Introduction

It is widely accepted that anthropogenic influence is almost ubiquitous to ecosystems across the globe, altering long-standing ecological processes and threatening many wildlife species (Boyes et al., 2019; Dirzo et al., 2014; Finn et al., 2023; Jiguet et al., 2007). Subsequent ramifications are already being documented, collectively prompting significant shifts in phenological, distributional and physiological regimes (Jiguet et al., 2007). The present uptick in population declines further characterize the deleterious effects of human disturbance, the rate of extinction analogous to the past five mass extinction events, emphasized by the unprecedented timescale upon which extinctions have been occurring (Dirzo et al., 2014; Finn et al., 2023). Defaunation, the term used to describe the accelerated loss of wildlife diversity, threatens ecosystem functioning through the absence of ecological roles (Dirzo et al., 2014; Finn et al., 2023). Extinction also operates on a local-scale, wherein species are extirpated from local areas resulting in more immediate consequences that are often hidden by large-scale status trends (Dirzo et al., 2014) and results in biotic homogenization across ecosystems (Boyes et al., 2019). Alarmingly, these small-scale changes are difficult to detect and are typically intermittent in nature (Boyes et al., 2019; Dirzo et al., 2014).

Beyond ecological impacts, defaunation has important implications for human well-being. Ecosystem services, or benefits for humans provided by wildlife species, are contingent upon the preservation of the wildlife species that shape them. For instance, services provisioned by wildlife such as pollination, biological pest control, nutrient cycling and nutritional acquisition, underlie the foundation of human society, the loss of which could contribute to significant economic and human-health consequences (Dirzo et al., 2014).

However, population responses to anthropogenic change are heterogeneous across wildlife species, with trends ultimately falling into one of two outcomes: colloquial ‘winners’ or ‘losers’; the former exhibiting population increases or stability, while the latter succumbs to population declines (Boyes et al., 2019). It has been found that wildlife species presently experiencing the greatest population losses typically exhibit one or a combination of several distinct life-history characteristics, the most common being: small geographic range size, low reproductive rates, large home range size and large body size (Dirzo et al., 2014). Other studies rely on gradients of range size, local abundance and habitat breadth to evaluate extinction risk (Boyes et al., 2019). Due to the phylogenetic evolution of life-history characteristics, population decreases tend to vary by taxonomic assignment, wherein different taxon experience disproportionate extinction risk (Leidner A. K., & Neel M. C., 2011). Drivers of population loss appear to be twofold in operation, wherein the risk of extinction is not only a function of species ecology but also a consequence of the type of anthropogenic perturbation (Dirzo et al., 2014). For example, threats such as habitat destruction and climate disruption create dissimilar ecological impacts, engendering disparate impacts to wildlife (Dirzo et al., 2014). Due to the nuanced and interconnected mechanisms of population decline, comprehensive drivers of extinction are difficult to identify and are highly-context dependent (Hardesty-Moore et al., 2018).

Migratory songbirds, a group experiencing significant global declines, are at the forefront of conservation concern (Kirby et al., 2008). Approximately 28% of migratory bird populations in North America have been lost in the last 50 years (Rosenberg et al., 2019). Migratory birds inhabit and depend upon multiple ecosystems, including those at breeding and wintering grounds as well as locations along their migratory route, inherently increasing the risk of experiencing ecological disturbance in one or more of the habitats (Zurell et al., 2018). Additionally, migration exposes birds to novel threats such as predation, adverse weather events and lack of food resources (Paxton et al., 2017). Invasive species, pollution, habitat degradation, habitat fragmentation, extreme climatic events and building collisions are a portion of human impacts threatening migratory birds (Nemes et al., 2023).

Bird-building collisions account for one of the greatest sources of anthropogenic bird mortality, resulting in an estimated one billion bird deaths annually (Klem, Jr. D 2008; Loss et al., 2014). Migratory birds appear to be disproportionately vulnerable to collision-related mortality events, which has been implicated to be due to their reliance upon celestial light for migratory navigation (Cabrera-Cruz et al., 2018; Borden et al., 2010; Loss et al., 2014). Given the continued expansion of urbanization, light pollution has increased, likely interfering with migratory birds' visual perception of navigational celestial cues and thus resulting in disorientation (Hölker et al., 2010; Longcore T. & C. Rich, 2004). Studies have reported false attractant effects of artificial light at night at multiple scales, wherein both local and regional bird densities have been positively correlated with artificial light sources, exacerbating collision risk (Guo et al., 2024, Hager et al., 2017; La Sorte et al., 2017, McLaren et al., 2018). Like many anthropogenic impacts, distinct drivers of bird-building collisions remain enigmatic as mortality appears to be a function of related and diverse mechanisms (Elmore et al., 2020; Loss et al., 2019). Most studies implicate one or a combination of the following factors in the increased risk of collision: building attributes, environmental conditions, and phylogeny of the bird. Specifically, context dependent building features such as reflective glass windows, total lighted area, structural height, adjacent vegetation and proximity to greenspace have been associated with collision risk (Calvin et al., 2010; Ocampo-Peñuela et al., 2016). Ecology of the respective species has also been posited to contribute to collisions, wherein those species that commonly migrate in mixed-species flocks are more likely to collide with buildings (Winger et al., 2019). Additionally, phylogenetic grouping may play a role, wherein insectivorous and woodland species have been found to have elevated collision mortalities (Elmore et al., 2020). Multiple studies have provided insight into those attributes that render a particular group of songbirds sensitive to anthropogenic environmental change, begging the question, what characteristics imbue a songbird with resilience to such changes?

Although less numerous, an increasing number of studies have begun to investigate drivers of species resilience within ‘winner’ species (Boyes et al., 2019). Traits such as high thermal tolerance, habitat generalism, increased natal dispersal and behavioral flexibility have been associated with global-change resilience (Jiguet et al., 2007; Vedder et al., 2013). Life-history characteristics that facilitate behavioral flexibility such as opportunistic or multivoltine reproduction events may also imbue resilience as they increase the ability of a species to respond to novel environmental conditions (Vedder et al., 2013). Resilience predictions often overlook both adaptive evolution and phenotypic plasticity, which may further extend the survival capacity of an organism in an increasingly modified environment (Vedder et al., 2013). Due to the immediate temporal scale upon which phenotypic plasticity acts, it may function as the primary predictor of climate change resilience. Improving understanding of drivers of population growth and range expansion can offer insight into drivers of extinction and in turn, inform future strategies aimed at increasing resilience for more sensitive species (Boyes et al., 2019). Additional consideration of wildlife ‘winners’ is necessary given their increased prevalence across the landscape as ecological processes are likely to shift due to modified community compositions (Boyes et al. 2019).

Traits such as increased thermal tolerance and behavioral flexibility also are likely to imbue some species with greater capacity for range expansion (Beever et al., 2011). Typically a result of population change at the local-scale, range dynamics are also driven by novel anthropogenic change (Dirzo et al., 2014). Factors such as habitat modification, resource subsidization and climatic change impact a species' range extent and may facilitate range shifts (La Sorte F. A., 2006; Tingley et al., 2012). Modified range dynamics can have immediate consequences as range reductions contribute to local-extinction and range expansion result in increasingly novel community assemblages (La Sorte F. A., 2006).

One species that has exhibited both population increase and range expansion despite the pervasive impacts of urbanization and climate change is the Northern Cardinal (*Cardinalis cardinalis*) (Dow & Scott 1971; Halkin et al., 2021). The eastern subspecies, *Cardinalis cardinalis cardinalis*, was once constrained to the eastern portion of the United States. This is in contrast to the broad extent of the present population, reaching northward to portions of Canada (Halkin et al., 2021). Cardinals are notable in that they exhibit many characteristics commonly associated with other wildlife ‘winners’ (Boyes et al. 2019). Cardinals have demonstrated plastic food foraging behaviors. Anecdotal evidence suggests that they opportunistically exploit human subsidized food resources such as backyard bird feeders, sustaining populations during periods of low natural food resource availability (Martin T.E. 1987, Morneau et al. 1999, Robb et al. 2008a, Robb et al. 2008b). Moreover, cardinals are less likely to experience mismatches in nutritional resource availability given their relatively low reliance on seasonal invertebrate food resources relative to more insectivorous passerines. Other studies posit that increased thermal tolerance via flexible metabolic thresholds is primarily responsible for the cardinal's success and likely continues to constrain their northernmost range extent (Canterbury 2002; Meehan et al., 2004; Root 1988). That said, there is no conclusive evidence identifying the primary driver of the cardinal's population increase or range expansion.

Here, my graduate research thesis investigates the nuanced and dynamic ways in which anthropogenic changes effect wildlife species. Collectively, my projects aim to focus on the heterogeneous responses of wildlife to anthropogenization by (1) creating novel methods to prevent migratory songbird collisions, as well as (2) study drivers of the Northern Cardinal range expansion. By studying both a wildlife 'loser' and a wildlife 'winner' within the context of anthropogenic impact, scientists are better able to develop conservation strategies for the 'losers' while gaining a more holistic and nuanced understanding of how 'winners' have adapted to global change (Boyes et al. 2019). As species populations and distributions continue to change, understanding how novel wildlife assemblages alter ecosystem services and affect human populations represents an important line of future inquiry (Boyes et al., 2019).

2 Climatic, temporal, and dietary constraints on the Northern Cardinal’s northward range expansion in human-dominated landscapes.

2.1 Introduction

Conservation science often aims to pinpoint the factors contributing to the decline of vulnerable wildlife species and then use these insights to develop strategies for their recovery. Conversely, wildlife populations that have expanded within human-dominated landscapes can offer insights into the underlying drivers of resilience (Boyes et al. 2019; Donihue & Lambert 2014; Jiquet et al. 2007). Having undergone recent range expansion (Dow & Scott 1971; Halkin & Linville 1999), the eastern subspecies of the Northern Cardinal (*Cardinalis cardinalis cardinalis*) serves as a model organism to identify the factors that facilitated rapid range expansion across novel and varied environments, as well as those factors that limited expansion at the peripheries of the expansion front (Sexton et al., 2009). Once exclusive to regions south of Ohio and Pennsylvania, the *cardinalis* subspecies’ range now extends north to portions of Canada, encompassing a wide breadth of ecosystems with a diverse array of climatic conditions (Beddall, 1963; Dow & Scott 1971; Halkin & Linville 1999). Further, 17 additional subspecies collectively occupy portions of the western United States, Mexico and Belize (Halkin et al., 2021).

Despite its ubiquitous presence across the Americas, the specific environmental conditions that both facilitated and constrained its range expansion remain poorly understood. Anecdotal evidence suggests that the Northern Cardinal's success is likely linked to their use of backyard bird feeders, a factor that has also been proposed to contribute to the population increases observed in various bird species worldwide (Martin T.E. 1987; Morneau et al. 1999; Robb et al. 2008a; Robb et al. 2008b). Reliance on backyard bird feeders may help populations endure periods of natural food scarcity, mitigating inherent nutritional limitations and supporting increased energy needs in colder and more northerly climates (Brittingham & Temple 1988; Oro et al. 2013;

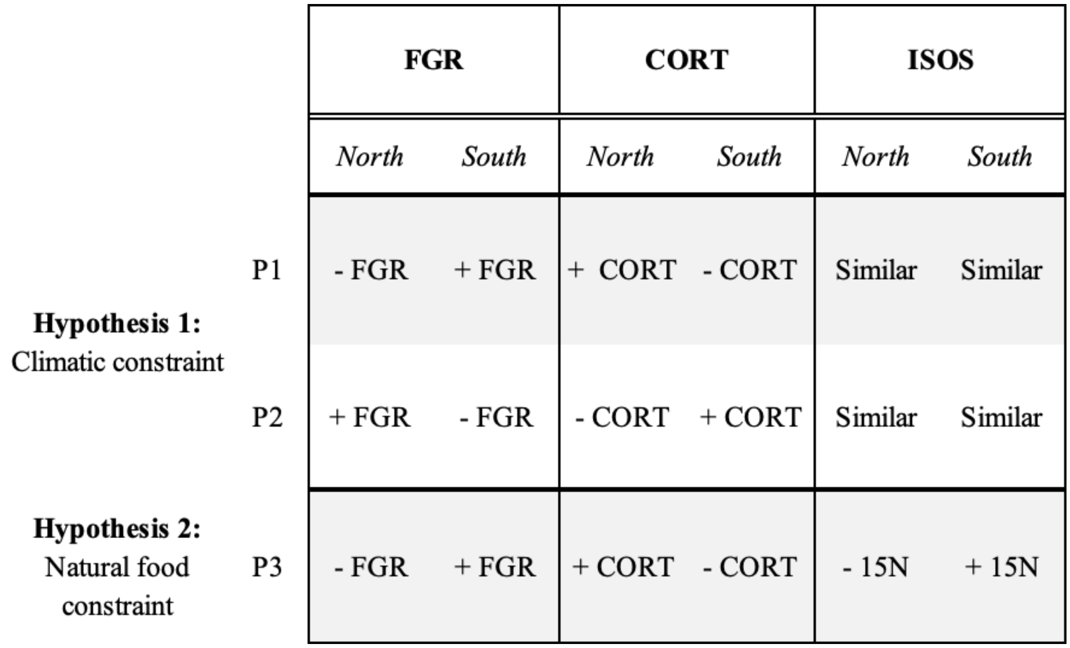
Plummer et al. 2018). However, backyard bird feeders in dense urban environments exist well north of the cardinal’s current expansion front, begging the question: what factors limit their further spread northward?

The Northern Cardinal’s ability to persist in diverse environments may also be attributed to temporal flexibility of life cycle events and energetics. For instance, non-migratory birds must breed, raise young and molt within a finite time period to optimize both reproductive output and survival (Boyle et al. 2015; Callery et al. 2022; Dawson A. 2007; Martin T. E. 1987; Svensson & Nilsen 1997). Variation in timing and duration of these life cycle events has been observed in species with ranges that encompass a wide breadth of environmental conditions (Holmes, R. T., 1971; Terrill, R. T., 2018). Intraspecific variation in the timing of life cycle events likely reflects evolutionary or behavioral fine-tuning to maximize fitness within a given environment. In general, species avoid overlapping energetically taxing lifecycle events, such as molt and breeding. Molt duration has been found to display a significant amount of variation across a single species range, reflecting dissimilar temporal constraints effectuated by variation in the onset of cold autumn and winter conditions (Holmes, R. T., 1971; Terrill, R. T., 2018).

At the forefront of the cardinal’s range expansion, I posited two non-mutually exclusive mechanisms that limit continued northward spread of cardinals. Firstly, the climatic constraint hypothesis suggests that longer and colder winters in the northern limits of the expansion front likely impose severe fitness consequences, acting through either: 1) reduced surplus energy stores for their annual molt due to thermoregulatory demands, resulting in prolonged autumn molt durations and increased stress (P1), or 2) reduced temporal windows for molt resulting in earlier and accelerated autumn molt durations and decreased external stress responses to avoid overlapping molt with early winter periods (P2) (Table 1). These respective predictions are distinguished by differential proximate mechanisms, wherein molt is limited by energy stores or conversely, temporal thresholds, however both predictions are bounded by climatic constraints. Second, the natural food constraint hypothesis (P3) suggests that cardinals cannot subsist solely on supplementary feeding and must depend on invertebrates and naturally occurring fruits during energyintensive periods like the autumn molt (Table 1). Consequently, the limited availability of these essential natural food resources during such critical times may restrict their northern progression through subsequent fitness consequences and increased nutritional stress levels. I anticipate that these constraints will result in measurable distinctions in molt velocity via feather growth rate (FGR), stress response through corticosterone accumulation (CORT) and dietary regimes via isotopic analysis (ISOS) from feathers sampled across the cardinal's range; the combination of each resulting measure reflecting a unique driving mechanism. This integrated approach, merging techniques often used in isolation, provides an opportunity to evaluate each hypothesis, enabling an appraisal of both climatic and food-related constraints.

Table 1. Matrix of postulated molt characteristics and diet regimes for each respective prediction (P1, P2, P3) across a latitudinal gradient of the eastern subspecies of the

Northern Cardinal. Measures include feather growth rate (FGR), corticosterone accumulation (CORT), and isotopic signatures (ISOS), with the unique combination of each reflecting a distinct mechanism of the Northern Cardinal’s northward range limitation. P1 posits slower FGR in the North due to increased energetic demands, increased CORT in the North due to increased climatic stress, and no difference in isotopic niche due to similar nutritional regimes. P2 posits faster FGR in the North to complete molt before the onset of harsh winter conditions, decreased CORT levels in the North to facilitate protein synthesis for fast FGR, and no difference in isotopic niche because nutritional regimes are similar. P3 posits slower FGR in the North due to decreased natural food resources and thus energetic resources, increased CORT levels in the North due to inadequate nutritional resources, and decreased δ15N isotopic levels in the North due to decreased access to secondary and tertiary consumers such as insects and spiders.



		FGR		**CORT**		**ISOS**	
		North	*South*	*North*	*South*	*North*	*South*
Hypothesis 1: Climatic constraint	P1	- FGR	+ FGR	+ CORT	- CORT	Similar	Similar
	P2	+ FGR	- FGR	- CORT	+ CORT	Similar	Similar
Hypothesis 2: Natural food constraint	P3	- FGR	+ FGR	+ CORT	- CORT	- 15N	+ 15N

2.2 Methods

2.2.1 Study Area

Feather samples were collected from three different study locations at varying latitudes, representing the latitudinal range of the eastern subspecies of the Northern Cardinal (*Cardinalis cardinalis cardinalis*). These locations included: Houghton, Michigan (MI); Oswego, New York (NY) and Baton Rouge, Louisiana (LA). Feather samples were also collected from a distinct western subspecies (*Cardinalis cardinalis canicaudus*) in San Antonio, Texas (TX) (Halkin et al., 2021) for comparative purposes. Each study area reflects dissimilar autumn climates, during which molt and subsequent feather growth occurs. Located along the northernmost front of the cardinal's range and characterized by long winters, Houghton exists at the furthest most extent of the *cardinalis* subspecies range and has the coldest average fall temperatures. In contrast, Baton Rouge, located within the southern portion of the *cardinalis* subspecies' North American range, has relatively mild fall temperatures. Fall precipitation is on average, highest in Oswego (Table 2). Climatic conditions experienced by the *canicaudus* subspecies in San Antonio are hotter and drier relative to overall conditions experienced by the *cardinalis* subspecies (Table 2).

Table 2. Average climate data for our study locations: Houghton, Michigan; Oswego, New York; Baton Rouge, Louisiana and San Antonio, Texas. Data represents the average indices for the month of September from 1991 to 2021. Data source is derived from ECMWF Data via *ClimateData.org*.

Location	**Subspecies**	**Latitude**	**Fall low temp.**	**Fall high temp.**	**Fall precip.**
Houghton	*C. c. cardinalis*	47.1211°N	13.4°C	19.6°C	95 mm
Oswego	*C. c. cardinalis*	43.4553°N	13.8°C	21.7°C	105 mm
Baton Rouge	*C. c. cardinalis*	30.4515°N	21.6°C	30.5°C	99 mm
San Antonio	*C. c. canicaudus*	29.4252°N	22.3°C	31.9°C	80 mm

2.2.2 Field Methods

My collaborators and I used mist-nets to capture, band, and collect samples from cardinals in MI, NY, LA and TX, during the summer and fall periods of 2019 to 2024. Specifically, once an individual cardinal was captured, I collected the right outer rectrix (R6) feather from each cardinal. In order to obtain the feather sample, the bird was held in a bander's grip and R6 was pulled in one fast short motion then placed in a small manila coin envelope. The envelopes were labeled with the date, location and band number. As feathers are relatively stable, no special precautions regarding their storage environment were needed. 20 samples were collected from NY and TX, 60 samples were collected from LA and 4 samples were collected from MI. NY and LA samples were distributed across 2021 and 2022, whereas TX samples were distributed across 2022 and 2023. MI samples were collected in 2019, 2022 and 2024.

2.2.3 Ptilochronology

I measured the average feather growth rate through the process of ptilochronology. This technique involves measuring the width of growth bars within the rachis denoted by intervals of light and dark barbule bands, which approximately reflect 24 hours of growth. To execute the analysis, I followed ptilochronology protocols adapted from T. Grubb Jr, (1989). Growth bars in each feather were counted and the total length of the detectable growth bars were measured with a digital caliper. To standardize measures, the total length of the growth bars was divided by the total number of growth bars in each respective feather to obtain the average growth in mm per day.

2.2.4 Isotopic analysis

After ptilochronology was completed, feathers were prepared for isotopic analysis using a mass spectrometer following standard protocols (Chew et al. 2019). To clean the samples, feathers were dipped into a 2:1 chloroform to methanol solution for 30 seconds and subsequently stirred in three separate beakers of deionized water. Each feather was placed on clean paper towels to dry for 24-36 hours. Next, samples were measured, cut into 0.60 µg sample weights and packaged in tin capsules. This was executed by cutting off the right portion of the calamus approximately one centimeter from the tip with a clean razor blade. Using clean forceps, the cut sample was placed on a tared microbalance to be weighed. Small portions of the sample were cut off until the weight was within the desired parameters (+/- 0.05 µg). Relative abundances of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were determined on a Thermo Scientific ConfloIV Interface and Delta V Continuous Flow-Stable Isotope Ratio Mass Spectrometer. The results are expressed in standard delta notation (δ), defined as parts per thousand (‰) as follows: $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where R is the ratio of heavy to light isotope in the sample and standard respectively (Coplen, 2011; Peterson & Fry 1987). IAEA, USGS, and NIST certified isotopic standards were run at the beginning of the analysis. One certified standard is also run at the end of the analysis to check for stability of the calibration. An internal standard was run every 10 samples. The precision of the certified isotopic standards was typically between 0.2 to 0.5‰.

2.2.5 Corticosterone

To quantitatively measure stress, I analyzed corticosterone accumulation (CORT) from the same set of feathers. Analysis was completed with the remaining vane portion of the feather after isotopic analysis preparation. For each feather, the mass was recorded (± 0.001mg) and the length (± 0.1 mm). Remnants of the calamus were cut off at the base of the vane, so that only the vane remained, the remaining sample was minced into small pieces. Dr. Christopher Tonra quantified feather CORT at Ohio State University using a methanol-based extraction, modified from Bortolotti et al. (2008), and a commercial ELISA kit (Corticosterone ELISA kit; Neogen Corporation, Ayr, UK) as validated by Carbajal et al. (2014). The methanol extraction was achieved by incubating the minced feather in methanol (HPLC grade) overnight, vacuum filtration, and evaporating under

N2 gas. Samples were then reconstituted following Corticosterone ELISA kit directions. Inter-assay variation based on the coefficient of variation (%CV) of relative binding of kit standards was 11.4% and intra-assay variation based on the average %CV between the duplicate unknown samples was 4.9%. Extracts were separated from solids using vacuum filtration, evaporated under nitrogen gas, then reconstituted in Neogen extraction and run through ELISA kit procedures. Assay recovery was assessed by adding 20µL of tritium-labeled CORT in each sample and using a scintillation counter.

2.2.6 Statistical analysis

Due to the uneven sample size across sample locations, I conducted a bootstrap analysis where I randomly selected with replacement FGR and CORT samples (n=5000) from the NY, LA, and TX study areas study to create comparative distributions. I did not bootstrap samples from MI due to small sample sizes. I used the program R function “randomLAM” to run the 5000 permutations and to calculate 95% confidence intervals for each distribution (R Development Core Team 2022). Single values determined from Houghton samples were then compared to each study area’s 95% confidence interval to evaluate statistical differences. I also conducted ANOVA tests using the program R function “aov” on the effect of location and year on FGR and CORT accumulation individually. I included a nested random effect of sex by location to account for non-location-based variation. To corroborate the inclusion of the random effect, I also conducted an ANOVA for the effect of location on sex. Shapiro-Wilkes test was conducted to confirm data normality. Isotopic niche positions for each location were determined by creating stable isotopic biplots that reflected the mean $\delta^{13}C$ and $\delta^{15}N$ ‰ values and associated standard errors. Isotopic results were also analyzed using an ANOVA test for the effect of location on $\delta^{15}N$ and $\delta^{13}C$ values respectively (R Development Core Team 2022).

2.3 Results

2.3.1 Feather Growth Rate

My ANOVA analysis indicated a significant effect of location on feather growth rate ($F_{3,3} = 11.82$, $P = 0.0361$). Within the eastern subspecies, Michigan samples showed the fastest growth rate, followed New York, then Louisiana samples (Table 3; Figure 1). Houghton samples had the largest variation in feather growth rate relative to both the New York and Louisiana samples (Table 3). The Texas subspecies, *Cardinalis cardinalis canicaudus*, had feather growth rates similar to those found in Houghton, MI samples (Figure 2). Additionally, I found a significant effect of sex on feather growth rate, wherein females displayed faster growth rates relative to males across all four sample locations (ANOVA $F_{1, 1o1} = 4.609$, $P = 0.0342$; Table 4). Year did not have a significant effect on feather growth rate (ANOVA $F_{1, 95} = 0.907$, $P = 0.441$). Shapiro-Wilkes test indicated that the data had an approximately normal distribution ($W = 0.991$, $P = 0.6775$).

Table 3. Means and standard errors of feather growth rate (FGR) (mm/day) from each study location. We analyzed a total of 107 Northern Cardinal feathers representing two distinct subspecies, (*Cardinalis cardinalis cardinalis* and *Cardinalis cardinalis canicaudus*) and four locations including: San Antonio, Texas; Baton Rouge, Louisiana; Oswego, New York; and Houghton, Michigan. 59 samples were measured from Louisiana, 20 from New York, 20 from Texas and 4 from Michigan.

Location	**Subspecies**	**Latitude**	**Feather growth rate (mm/day)**
Houghton, Michigan	*C. c. cardinalis*	47.1211°N	3.643 ± 0.146
Oswego, New York	*C. c. cardinalis*	43.4553°N	3.504 ± 0.074
Baton Rouge, Louisiana	*C. c. cardinalis*	30.4515°N	3.384 ± 0.037
San Antonio, Texas	*C. c. canicaudus*	29.4252°N	3.592 ± 0.066

Table 4. Means and standard errors of feather growth rate (days/mm) by sex from each study location. We analyzed a total of 107 Northern Cardinal feathers representing two distinct subspecies, (*Cardinalis cardinalis cardinalis* and *Cardinalis cardinalis canicaudus*) and four locations including: San Antonio, Texas; Baton Rouge, Louisiana; Oswego, New York; and Houghton, Michigan. 59 samples were measured from Louisiana, 20 from New York, 20 from Texas and 4 from Michigan.

Sex	**Michigan**	**New York**	**Louisiana**	**Texas**
Female	3.715 ± 0.165	3.642 ± 0.111	3.482 ± 0.054	3.604 ± 0.081
Male	3.570 ± 0.300	3.459 ± 0.094	3.303 ± 0.054	3.582 ± 0.109

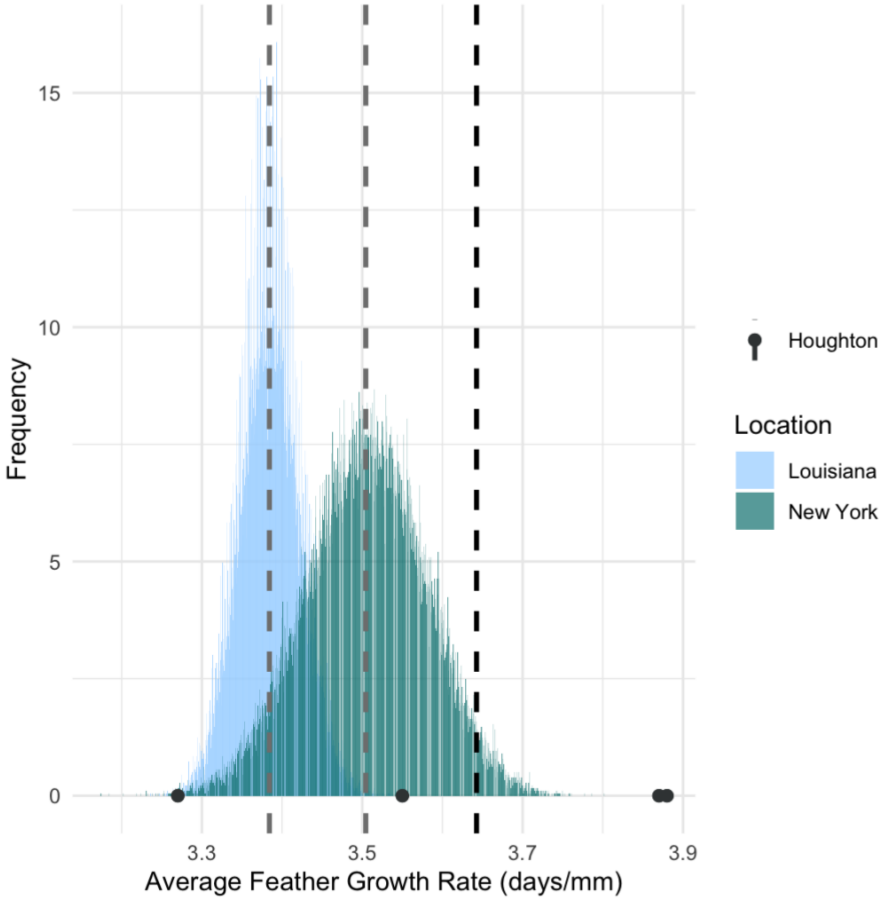


Figure 1. Comparative bootstrapped distributions with 5000 permutations for feather growth rate of the *Cardinalis cardinalis cardinalis* subspecies (days/mm) by study location (LA, NY). Dashed lines represent distribution means. Samples from Houghton, Michigan were limited (n = 4) and were thus plotted as points representing actual values.

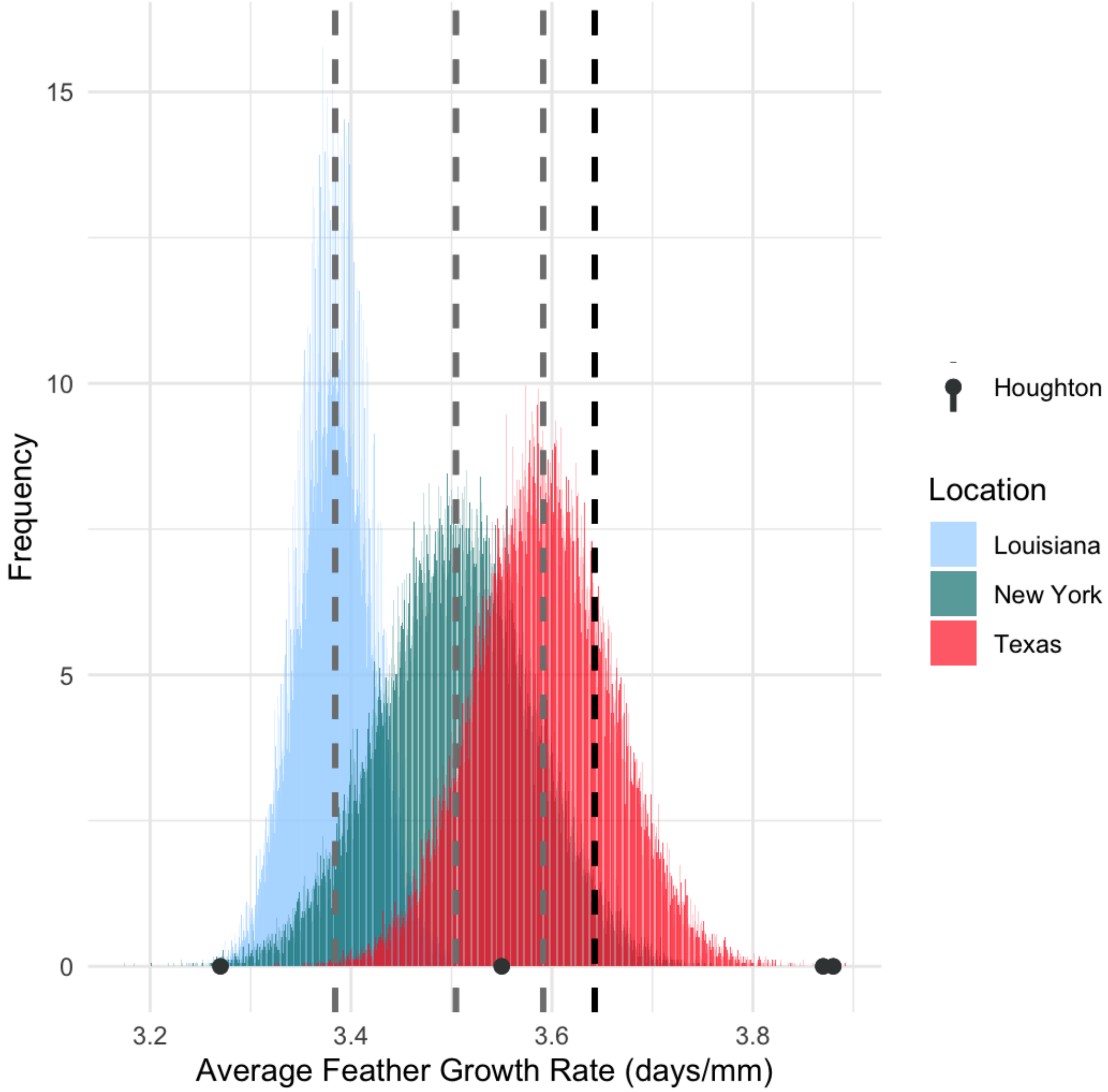


Figure 2. Comparative bootstrapped distributions across study locations with 5000 permutations for feather growth rate (days/mm) for all samples including the *Cardinalis cardinalis canicaudus* subspecies in TX. Dashed lines are distribution means. Samples from Houghton, Michigan were limited (n = 4) and were thus plotted as points representing actual values.

2.3.2 Corticosterone

Means from the bootstrapped comparative distributions indicated significant variation in CORT totals in New York and Louisiana samples, Louisiana samples reporting larger CORT accruements relative to New York samples (Table 5; Figure 3). Houghton, Michigan samples were on average, similar to New York CORT totals. Houghton samples also included a large amount of variation, values ranging from 6.490 to 92.402 pg/mg, representing the lowest and highest CORT totals, respectively (Figure 3). The Texas subspecies, *Cardinalis cardinalis canicaudus*, had CORT totals similar to those found in Louisiana samples (Figure 4). The ANOVA from data before the bootstrap transformation did not indicate a significant effect of location or sex on CORT (ANOVA $F_{2,42} = 0.342$, $P = 0.712$).

Table 5. Corticosterone total (CORT) means and standard errors from randomized sampling distributions of New York, Louisiana, and Texas with 5,000 permutations. Michigan mean and standard error values represent actual data points as these samples were not boostrapped given the small sample size (4). A total of 68 Northern Cardinal feathers representing two distinct subspecies, (*Cardinalis cardinalis cardinalis* and *Cardinalis cardinalis canicaudus*) and four locations were sampled including: San Antonio, Texas; Baton Rouge, Louisiana; Oswego, New York; and Houghton, Michigan. 22 samples were measured from Louisiana, 18 from New York, 20 from Texas and 4 from Michigan.

Location	**Subspecies**	**Latitude**	**CORT**
Houghton, Michigan	*C. c. cardinalis*	47.1211°N	43.454 ± 20.463
Oswego, New York	*C. c. cardinalis*	43.4553°N	40.935 ± 2.977
Baton Rouge, Louisiana	*C. c. cardinalis*	30.4515°N	52.494 ± 5.024
San Antonio, Texas	*C. c. canicaudus*	29.4252°N	52.492 ± 5.242

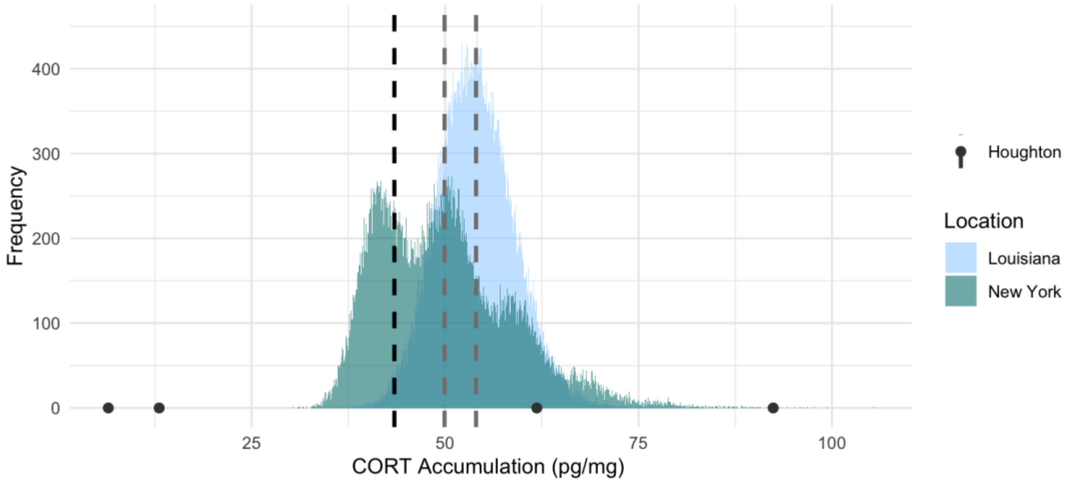


Figure 3. Comparative bootstrapped distributions with 5000 permutations for feather corticosterone accumulation (pg/mg) of the *Cardinalis cardinalis cardinalis* subspecies by study location (LA, NY). Samples from Houghton, Michigan were limited (n = 4) and were thus plotted as points representing actual values.

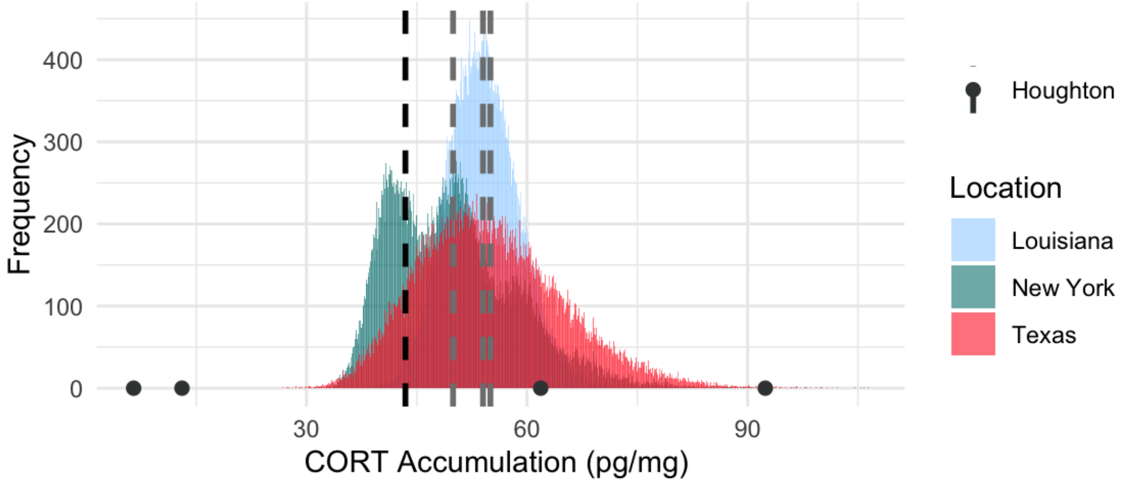


Figure 4. Comparative bootstrapped distributions across study locations with 5000 permutations for feather corticosterone accumulation (pg/mg) for all samples including the *Cardinalis cardinalis canicaudus* subspecies in TX. Samples from Houghton, Michigan were limited (n = 4) and were thus plotted as points representing actual values.

2.3.3 Stable Isotopes

Location did not show a significant effect on $\delta^{15}N$ values between Michigan, New York and Louisiana samples (Figure 5; ANOVA $F_{2, 36} = 1.144$, $P = 0.33$). However, when Texas samples were included in the model; location showed a significant effect (ANOVA $F_{3, 55} = 12.32$, $P < 0.001$; Table 6). Location had a slightly significant effect on $\delta^{13}C$ values between Michigan, New York and Louisiana samples (ANOVA $F_{2, 36} = 4.027$, $P = 0.026$; Table 7). Moreover, when Texas samples were included in the model; location showed a much stronger effect on $\delta^{13}C$ values (ANOVA $F_{3, 55} = 27.74$, $P < 0.001$) (Table 7; Figure 5).

Table 6. Means and standard errors of δ15N from each study location. A total of 64 Northern Cardinal feathers representing two distinct subspecies, (*Cardinalis cardinalis cardinalis* and *Cardinalis cardinalis canicaudus*) and four locations were sampled, including: San Antonio, Texas; Baton Rouge, Louisiana; Oswego, New York; and Houghton, Michigan. 20 samples were measured from Louisiana, 20 from New York, 20 from Texas and 4 from Michigan.

Location	**Subspecies**	**Latitude**	**δ15N**
Houghton, Michigan	*C. c. cardinalis*	47.1211°N	7.000 ± 0.286
Oswego, New York	*C. c. cardinalis*	43.4553°N	6.845 ± 0.239
Baton Rouge, Louisiana	*C. c. cardinalis*	30.4515°N	6.307 ± 0.343
San Antonio, Texas	*C. c. canicaudus*	29.4252°N	9.105 ± 0.445

Table 7. Means and standard errors of δ13C from each study location. A total of 64 Northern Cardinal feathers representing two distinct subspecies, (Cardinalis cardinalis cardinalis and Cardinalis cardinalis canicaudus) and four locations were sampled, including: San Antonio, Texas; Baton Rouge, Louisiana; Oswego, New York; and Houghton, Michigan. 20 samples were measured from Louisiana, 20 from New York, 20 from Texas and 4 from Michigan.

Location	**Subspecies**	**Latitude**	**δ13C**
Houghton, Michigan	*C. c. cardinalis*	47.1211°N	-23.075 ± 0.111
Oswego, New York	*C. c. cardinalis*	43.4553°N	-24.270 ± 0.260
Baton Rouge, Louisiana	*C. c. cardinalis*	30.4515°N	-23.393 ± 0.261
San Antonio, Texas	*C. c. canicaudus*	29.4252°N	-21.000 ± 0.302

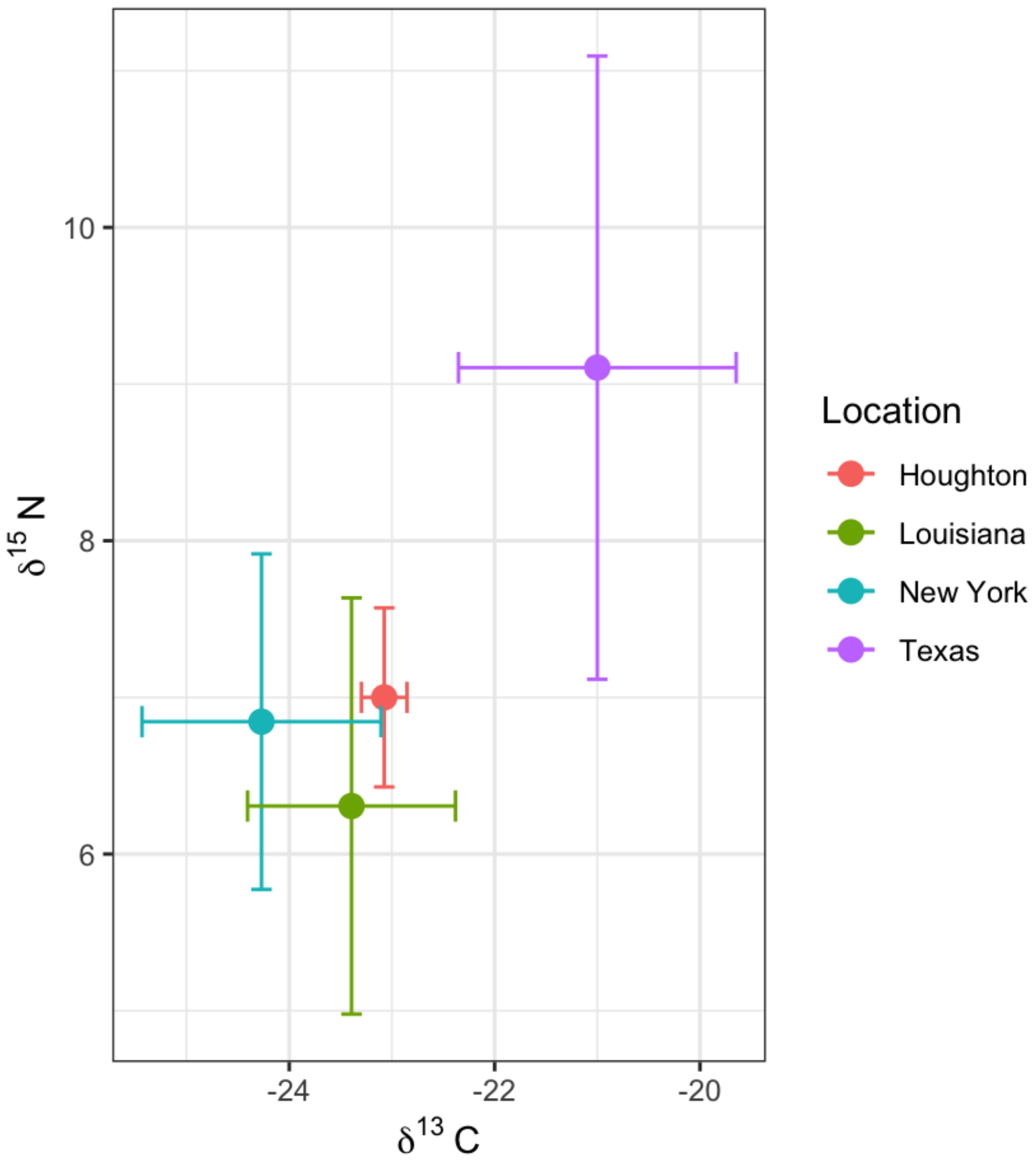


Figure 5. Stable isotope biplot indicating the mean δ^{13}C and δ^{15}N ‰ values of feather samples by study location) including both the *cardinalis* (Houghton, Louisiana, New York) and *canicaudus* (Texas) subspecies. Standard error is indicated by error bars.

2.4 Discussion

Resident bird populations are constrained by various temporal factors which are contingent upon climatic conditions and food resource availability (Boyle et al. 2015; Callery et al. 2022; Dawson A. 2007; Martin T. E. 1987; Svensson & Nilsen 1997). Anthropogenic influence across the globe has altered ecological processes intrinsically linked to these climatic and nutritional regimes, however the consequences have yet to be understood in detail (Boyes et al. 2019; Donihue & Lambert 2014; Jiquet et al. 2007). Having undergone recent range expansion, the eastern subspecies of the Northern Cardinal (*Cardinalis cardinalis cardinalis*), is a model organism to study dissimilar physiological responses when subjected to substantial environmental variation, to better understand how climate and nutritional limitations may affect their rapid range expansion (Dow & Scott 1971; Halkin & Linville 1999). Here, I employed a combination of stable isotope analysis, ptilochronology and corticosterone assays, from individuals encompassing the breadth of cardinals' eastern range to examine mechanisms of range expansion.

2.4.1 Stable Isotopes

Given that detectable differences in elemental-isotopic composition reflect dissimilarities in food resources being consumed and subsequently assimilated into an organism's integument (Kelly, J.F., 2000; Patrick et al. 2020), significant differences in isotopic niche of individuals along range edges would suggest important differences in food resource use and availability throughout the cardinal's range. However, within samples from the *Cardinalis cardinalis cardinalis* subspecies, I found that the $\delta^{15}N$ isotopic values from feathers grown during fall molt were relatively similar across this subspecies' range, suggesting that individuals forage at analogous trophic levels irrespective of location (Figure 5) (Inger & Bearhop, 2008; Kelly, J.F., 2000; Patrick et al. 2020). $\delta^{13}C$ values displayed some variance, indicating potentially differences in carbon food sources. Carbon values for common ingredients in birdseed including corn and millet typically fall between -15 and -10 ‰ (Lightfoot et al., 2016), whereas sunflower seed as well as most native Midwest plant materials report carbon values near -

30 ‰ (Winkler, 1996; Kelly et al., 1996). The subtle differences within my samples may also be a result of divergent $\delta^{13}C$ baseline values, wherein $\delta^{13}C$ within the local environment differs as a function of the unique conditions and systems (Kelly, J.F., 2000). Given that the carbon values within my samples were between the range of native plant species as well as birdseed items I was unable to determine the contribution of birdseed to individual's diets. Moreover, plausible diet items were not individually analyzed for reference to isotopic signatures found within the cardinals' feathers, thus my isotopic analysis does not identify unique diet items. However, the relative uniformity across the latitudinal range of the *cardinalis* subspecies may suggest a common reliance on birdseed during the energetically-taxing molt period.

Conversely, samples from the Texan subspecies *Cardinalis cardinalis canicaudus* displayed significantly different $\delta^{15}N$ and $\delta^{13}C$ values relative to isotopic signatures from the eastern subspecies (Figure 5). Specifically, *canicaudus* samples had lower mean $\delta^{13}C$ values and higher average $\delta^{15}N$ values. This suggests that this western subspecies exhibits dissimilar dietary patterns relative to its eastern counterparts. Specifically, lower $\delta^{13}C$ values may indicate increased reliance on C4 or CAM plants and insects, including maize, sugarcane and sorghum and dry, desert plant sources, respectively (González-Carcacía et al., 2020; Keeley & Rundel, 2003). Isotopic signatures for CAM and C4 plants are similar and thus are not distinguishable in my study. Increased $\delta^{15}N$ can indicate higher trophic level positioning or an elevated $\delta^{15}N$ baseline environment (Adams & Sterner, 2000; Kelly, J.F., 2000; Patrick et al. 2020). Despite the inability to conclusively discern relative contributions from each diet item due to the absence of environmental sampling, the marked isotopic difference displayed by the *canicaudus* subspecies is sufficient to suggest significant dissimilarities in food resource use relative to their eastern counterparts.

Additionally, the energetic source of feather growth should be considered when attempting to interpret isotopic signatures of feathers. There is observed modulation in energy source use across bird species, most notably during the breeding season wherein birds are classified as either capital or income breeders (Drent & Daan, 2002). This refers to a species' tendency to rely on energy stores or, instead, subsist on nutritional resources from sustained and frequent foraging incidences. This may also be relevant to the molting period and thus may affect the time period in which dietary inference from stable isotopes can be made.

2.4.2 Ptilochronology

Feather growth rate displayed significant variation by sex (Table 2). Specifically, females exhibited faster average feather growth rates relative to males across all four sample locations. Similar results have been previously found in Northern Cardinals (Grubb et al., 1991) as well as Barn Swallows (*Hirundo rustica*) (Saino et al., 2013). However, the mechanisms driving this pattern are not well understood. One explanation may be energetic discrepancies prior to molt initiation due to the prominent role females have in nest incubation during the preceding breeding season (Laskey, 1944; Verner & Wilson, 1969). Heat production for incubation is energetically costly and incubation reduces potential foraging opportunities necessary for caloric maintenance (Svensson & Nilsson, 1997). This may result in delayed molt initiation within females, in turn necessitating accelerated feather growth given impending winter weather (Svensson & Nilsson, 1997). Given that males generally obtain higher-quality food resources due to dominance behaviors (Laskey, 1944), these results further suggest factors beyond nutrition as drivers of feather growth rate.

When accounting for sex effects, feather growth rate was positively correlated with location, with the fastest average growth being in the northernmost populations (MI, NY) (Figure 1). Independent drivers of feather growth rate have been historically difficult to isolate, wherein nutrition, intra-specific competition and climate have all been found to play confounding roles (Grubb Jr, 1989; Grubb Jr & Cimprich 1990). In contradiction to my findings, it has been posited that energetic stress is associated with decreased feather growth rates due to decreased surplus energy stores for molt (Grubb Jr, 1989). However, if this was true for Northern Cardinals, feather growth rate would have decreased with latitude given increasingly limited food resources in northern environments. Instead, my results are more parsimonious with a small number of other studies that indicate variation in the pace of life cycle events as the primary driver of feather growth rate (Holmes 1971; Williamson and Emison 1971; Mewaldt and King 1978; Hemborg et al. 2001; Terrill, R. T., 2018). This is consistent with inter-specific patterns previously described by life history theory which states that life cycle events hasten with increased environmental seasonality. The gradient of climates encompassed within my study areas likely promotes dissimilar molt velocities across environments, wherein cardinals hasten feather growth in the north to accommodate shorter summer seasons (Terrill, R. T., 2018).

Additionally, cardinals nearer to the northern expansion front exhibited a greater variance in feather growth rate relative to cardinals in the heart of the range (Figure 1). Greater breadth in individual behavior at expansion fronts has been observed in wildlife populations, inferring greater likelihood of stabilization as the population responds to novel environmental conditions (Sexton et al., 2009; Sih et al., 2012). My study found that variation in life history traits differ at both the population level as well as the individual level within Northern Cardinals, wherein pioneering individuals at the leading edge of the range enter new habitats and experience environmental uncertainty, likely resulting in broader individual variation in feather growth rates. This may reflect a lineage level process of searching evolutionary and behavioral adaptive space for optimal timing and durations of molt to optimize fitness in new environments. This process likely resulted in the distinct gradient of variation as one moves from the expansion front in Michigan (highest variation in feather growth), to established populations in New York (intermediate variation in feather growth), through the core of the *cardinalis* subspecies' range in Louisiana (least variability in molt velocity) (Fig 1).

Feather growth rate also has implications for feather quality. In some cases, the structural integrity of the feather is compromised due to accelerated feather growth rate (Terrill, R. T., 2018). This has implications for cardinals along the expansion front as they likely face tradeoffs associated with feather quality and the preceding completion of reproductive events (Terrill, R. T., 2018). Interestingly, the Texas subspecies displayed feather growth rates comparable to the Michigan samples. This likely reflects relatively strong seasonality driven by prolonged dry periods, rather than the prolonged cold temperatures as experienced in Michigan. Additionally, comparisons may be confounded by phylogenetic differences between the *cardinalis* and *canicaudus* subspecies.

2.4.3 Corticosterone

My results suggest that corticosterone (CORT) accumulation was negatively correlated with latitude: lower in the expansion front and higher in the core of the species' range (Figure 3). A secretion of the hypothalamic-pituitary-adrenal gland, corticosterone is released within an organism's bloodstream in response to a perceived threat, triggering increased alertness, restlessness and evasion behaviors (Breuner et al., 2003; Bortolotti et al., 2008; Legagneux et al 2013). Given that northernmost cardinals experience greater climatic stressors, the negative correlation with latitude exhibited by my samples is in contradiction to the majority of the current literatures' findings, which posit CORT levels reflect various acute stressors including those associated with inadequate nutrition and climatic stress (Breuner et al., 2003; Bortolotti et al., 2008; Legagneux et al 2013).

However, there is some evidence that molt may strongly affect CORT accumulation, altering conventional stress response mechanisms. For instance, CORT accumulation has been found to vary with seasonal activities, specifically, CORT levels decrease during the molting period (Romero et al., 2005). This is implicated to be due to the deleterious effects CORT has on protein synthesis, a vital biological function of feather growth (Romero et al., 2005). Low CORT levels within northernmost individuals may also be a mechanistic response to chronic environmental stress (Astheimer et al., 2000; Rich & Romero, 2005). For example, decreased CORT levels have been observed in birds that are subject to long term exposure to stress, which may function to decrease negative physiological and immunological consequences associated with chronic CORT exposure (Astheimer et al., 2000; Rich & Romero, 2005). This is a reasonable explanation for my results, wherein individuals along the expansion front exhibit an increased tolerance for stress stimulants due to the relatively harsh northern environment. Additionally, intraspecific competition can attribute to increased secretion of CORT, which may reflect stress from resource limitations and increased aggression responses associated with exposure to conspecifics at my Louisiana study site (Braasch et al., 2014; Robertson et al., 2017).

Together, my results suggest that the Northern Cardinal's range is constrained by the temporal limits placed upon life cycle events. Similarity in isotopic niches of cardinals across latitudes suggest that dissimilarities in the autumn diet *does not* serve as a limiting factor preventing further northward expansion. This highlights the importance of birdseed within cardinals' diets across their range. These findings are consistent with my second of three postulated predictions, wherein feather growth rate increases with latitude, CORT accumulation decreases with latitude and isotopic niche is uniform across locations (Table 1). Specifically, the shorter summer seasons characteristic of high latitudes, likely exerts selective pressures on birds to hasten fall molt before the onset of cold winter conditions (Holmes, R. T., 1971; Terrill, R. T., 2018). The observed decrease in CORT levels with latitude may be a result of several mechanisms those being either, (1) physiological response to promote quick feather growth, (2) decreased intraspecific competition, (3) increased stress tolerance, or a combination of all three.

The heightened speed of molt along the cardinals' northern range likely exacerbates trade-offs in adult survival. Compromised feather quality reduces both predator evasion and thermoregulatory efficiency (Dawson et al., 2000; Jenni-Eiermann et al., 2015; Møller & Nielsen, 2018; Terrill, R. T., 2018), and decreased CORT levels weaken survival-promoting stress responses (Romero et al., 2005). In contrast, cardinals in the heart of their range have greater temporal breadth between breeding and molting behaviors thus enabling greater time investments to feather growth. This phenomenon highlights the remarkable capacity of the Northern Cardinal to modify energetic prioritization of critical life-history events in order to conform to climatic conditions across an expansive range. The mechanistic origin of the behavioral assimilation is yet to be fully understood, with evidence for both phenotypic expression and evolutionary adaptation (Donihue & Lambert, 2014; Miller et al., 2017).

This has further implications for the Northern Cardinal's range as global weather patterns continue to change. Specifically, as the overall mean climatic temperature increases, thermoregulatory demands during fall seasons will decrease, lifting energetic burdens from Northern Cardinals in the north and ostensibly permitting their continued northward expansion (Arnell et al., 2019). However, decreased precipitation along the western and southern portions of the cardinal’s range may limit the population along the southwestern range boundaries. Ultimately, plasticity in life history traits and physiological processes likely supports the heightened variation I observed in pioneering individuals, which may be key to adaptation and population-level resilience in the Anthropocene, a period characterized by rapid environmental change.

Likewise, proximate and ultimate consequences of human food subsidization to wildlife have yet to be fully understood, having thus far proven to be generally advantageous to cardinals (Oro et al. 2013). For instance, the continued expansion of the Northern Cardinal is likely contingent upon the continued subsidization of anthropogenic food, the cessation of which may be necessitated by novel disease pandemics such as the recent outbreak of avian influenza. At a regional scale, the discontinuation of provisioned birdseed would likely reinstate nutritional constraints, potentially resulting in the collapse of contemporary range extents and thus populations of birdseed-reliant species. These results speak to the nuanced and complex manners in which anthropogenic food supplementation interact with climate change to drive the emergence of novel wildlife assemblages across northerly latitudes.

3 Efficacy of acoustic signals as a solution to migratory bird-building collisions

3.1 Introduction

Facilitated by urbanization, the rapid expansion of artificial light at night (ALAN) has significantly altered the night skyscape to the detriment of many wildlife species (Hölker et al., 2010; Longcore T. & C. Rich, 2004). Interfering with circadian-based biological and ecological regimes, light pollution has disrupted behaviors and annual cycles such as nesting, foraging, and reproduction within a wide breadth of species (Cabrera-Cruz et al., 2018; Davide M. Dominoni 2015; Hölker et al., 2010). Navigating by aid of celestial bodies, migratory songbirds are particularly vulnerable to light pollution, because illuminated city-buildings cause disorientation, resulting in bird-building collisions (Cabrera-Cruz et al., 2018; Gauthreaux Jr et al, 2006). Recent evidence suggests that ALAN may even act as an attractant to migratory birds, artificially increasing avian abundance near urban areas at both the local and regional scale, thereby exacerbating collision mortalities (Guo et al., 2024, Hager et al., 2017; La Sorte et al., 2017, McLaren et al., 2018). These collisions cause as many as one billion bird fatalities each year, constituting two to nine percent of all birds in North America and making building-strikes the second largest source of human-caused avian mortality in the United States (Klem, Jr. D 2008; Loss et al, 2014).

Correlates of bird-building collisions are nuanced and complex and seem to be a function of a variety of interrelated factors regarding building structure as well as avian life-history patterns (Elmore et al., 2020; Hager et al., 2017; Loss et al., 2014; Loss et al., 2019; Ocampo-Peñuela et al., 2016). Notably, many studies have found total glass area on buildings to be positively correlated with bird collisions (Borden et al., 2010; Elmore et al., 2020; Loss et al., 2019). Other factors including building size, building height and adjacent vegetated cover have been implicated to increase mortality rates (Borden et al., 2010; Elmore et al., 2020; Hager et al., 2017). Ecological factors also appear to play a role in collisions. For example, it is commonly accepted that migratory birds, particularly wood-warblers, thrushes and native sparrows, constitute the greatest number of collisions, which may relate to their propensity for disorientation when encountering light pollution (Borden et al., 2010; Elmore et al., 2020; Hager et al., 2017; Loss et al., 2014; Ocampo-Peñuela et al., 2016). Faced with imminent threats of habitat loss in both breeding and wintering grounds, the reduction of building collisions along birds' migratory routes is critical for the preservation of their populations as well as the ecosystems they influence (Xu et al. 2020). Alarmingly, several species of high-collision risk have been identified as national Birds of Conservation Concern, wherein building-collisions are suspected to play a significant role in their population declines (Elmore et al., 2020; Loss et al., 2014).

Recent findings have begun to uncover the evolutionary adaptations involved in avian migratory orientation mechanisms, providing opportunity for the development of more effective collision mitigation strategies. In particular, there has been increasing evidence that birds may use heterospecific acoustic cues when determining migratory orientation and navigation as well as stopover habitat selection, which may reduce individual errors via collective decision making (Farnsworth & Lovette, 2008; Gayk et al., 2021; Hamilton W.J., 1962; Muckhin et al., 2008; Szymkowiak et al., 2017; Winger et al., 2019). In the spring, migratory songbirds have been known to preferentially select both stopover and breeding habitat sites when detecting songs from conspecifics or functionally-similar heterospecifics (Muckhin et al., 2008; Szymkowiak et al., 2017). Similarly, many species of migratory birds emit short, distinct sounds known as flight calls while traveling in mixed-species flocks (Farnsworth A., 2005; Farnsworth & Lovette, 2008; Gayk Z.G & D.J. Mennill, 2023; Watson et al., 2016). While the function of flight calls remains unclear, it is postulated that the acoustic cues may facilitate flock communication, contributing to flock cohesion and reducing disorientation particularly for inexperienced, young birds (Farnsworth A., 2005; Gayk Z.G & D.J. Mennill, 2023; Hamilton W.J., 1962; Smith et al 2014). Recent studies have found that the acoustic structure of flight calls within the wood-warbler (Parulid) family are correlated to migratory patterns, wherein species with similar migratory journeys exhibit acoustic convergence (Gayk et al., 2021; Gayk Z.G & D.J. Mennill, 2023). Moreover, unfavorable or novel environmental conditions such as impending precipitation and reduced visibility have been associated with increased flight call frequencies, suggesting that socially-derived acoustic cues may play a vital role in birds' navigational decisions and may be driven by strong selective forces (Farnsworth A., 2005; Smith et al 2014; Watson et al., 2016).

However, flight-calling behaviors are not uniform across migratory species. Some lineages don't utter flight calls, including tyrant flycatchers and vireos (Farnsworth A., 2005). Winger et al. (2019), found that flight calling behaviors were associated with vulnerability to building collisions subjected to ALAN, suggesting that the disorientating nature of lights may prompt social species to emit increased acoustic signals. These species have significantly higher collision rates than species that undergo solitary migratory journeys, implicating that increased vocalizations may artificially attract larger numbers of flight-calling birds and amplify collision mortalities (Winger et al., 2019).

Novel approaches to bird-collision mitigation have begun to incorporate findings from avian sensory ecology to create more effective deterrent devices (G. R. Martin, 2011). Presently, most deterrent attempts employ visual signals, however these are used with mixed success (Klem & Saenger, 2013). Historically used as pest-species mitigation, acoustic signals have only recently been identified as a plausible deterrent mechanism for migratory songbirds (Rivadeneira et al., 2018). Specifically, Boycott et al (2018) found that the projection of a 4-6 kHz frequency sound prompted evasive flight maneuvers from passing migratory birds near the base of a communication tower.

My project aimed to determine the capacity of an acoustic signal to manipulate migratory birds' airspace navigation and mitigate building collisions. Based on evidence that acoustic signals drive birds' migratory flight orientation (Boycott et al., 2018; Winger et al., 2019) I hypothesized that exposing migrating songbirds to several dissimilar acoustic cues will modify birds' flight paths, by either artificially attracting or deterring them from entering a given airspace. Specifically, I created three dissimilar noises: an attractant, an engineered deterrent, and a biological deterrent. Consisting of a mixed compilation of common migratory bird species songs, I expected the attractant to increase bird detections relative to background bird numbers. Conversely, I expected the two deterrent sounds to decrease bird detections relative to background bird numbers. I expected the engineered deterrent, a modulated sound that coincides with the frequency of common flight calls, being 2-10 kHz, to effectively disrupt flock communication, inhibiting their capacity to navigate using shared social information, thus indirectly causing deterrence away from the sound source. I expected the biological control, consisting of a compilation of common avian predators from across the Mississippi flyway, to alarm birds by mimicking relevant predatory threats, thus causing deterrence away from the sound source. Results from this project provide insight for the development of an acoustic product that can be deployed on buildings to mitigate avian mortality. While many projects have investigated the application of disruptive acoustic signals for the deterrence of nuisance bird species, my project is novel in that it is the first of my knowledge to apply acoustic manipulation to migratory songbirds in order to mitigate bird-building collisions by targeting socially-derived information.

3.2 Methods

3.2.1 Study Area

Collectively, experiments were conducted at three different locations over the course of 1.5 years (August 2022, April 2023 and September 2023). Both the preliminary and the subsequent spring experiment were located within the Keweenaw Peninsula. The Keweenaw is the northernmost portion of the Upper Peninsula of Michigan and is bordered by Lake Superior on both sides. The area is largely rural with few small towns and is characterized by its continuous swaths of predominantly maple-hemlock forests. The peninsula acts as a critical migratory corridor, bridging a large expanse of Lake Superior and connecting the Mississippi Flyway from Canada to Michigan (Youngman et al., 2017). My final fall speaker deployment was located just north of Chicago, Illinois at

Northwestern University's Evanston campus. A sprawling, urban metropolis, Chicago records the largest number of bird-building collisions each year in North America and is also a critical component of the Mississippi Flyway (Van Doren et al., 2021). I conducted my experiments at two different buildings with large installments of windows, which have previously been observed to have high collision mortalities.

3.2.2 Preliminary Deterrent and Attractant: Fall 2022

To determine whether migratory songbird density could be manipulated by the alteration of the local soundscape, I conducted a three-part study over three migration seasons: Fall 2022, Spring 2023, and Fall 2023, in the Great Lakes region. To gain a basic understanding of birds' responses to broadcast acoustic signals, in fall 2022 (August 18, 2022 - September 17, 2022) I established two bird banding stations at two spatially independent, yet ecologically similar sites along the Portage Canal, a major body of water located in the Keweenaw Peninsula. The sites were located at Nara Nature Park (nara) and Pilgrim River Sloughs Boat Access (sloughs) and were approximately 6 km apart. I deployed two speaker units on simultaneous nights at each of the banding stations. The speakers emitted either a 6-8 kHz modulated frequency deterrent sound interspersed with a track of a Merlin (*Falco columbarius),* a common predator, or a track with common migratory bird species songs and flight calls that served as an attractant from 2:00 AM to 9:45 AM during peak migration flight times. To assess changes in songbird density, I captured birds in mist nets in the subsequent mornings, recording relative species abundance for 5 days. To account for inherent site differences, I changed the location of the acoustic sounds and repeated the treatment for 5 days, followed by an additional 5 control days wherein no acoustic treatment was applied.

3.2.3 Predator and Synthetic Deterrent: Spring 2023

Based on my preliminary results, I conducted another experiment in the following migration season (Spring 2023) to refine the acoustic deterrent and improve the capacity to dissuade migratory birds from entering unsafe airspace. Specifically, I separated the modulated frequency sound and the predator call, allowing for the evaluation of each respective sound as a potential deterrence signal. Additionally, I modified the frequency sound to include a greater white noise component and encompass a greater breadth of frequencies (2-10kHz). Each sound was broadcast at 70 dB, 50 meters from the speaker.

To achieve estimates of bird abundance, I deployed an autonomous recording unit (ARU) (Venier et al. 2012) at a remote, forested meadow in the Keweenaw Peninsula where I set up a speaker unit that broadcast my designed sounds. The speaker unit emitted either the 2-10 kHz modulated frequency sound or the track with a common predator call from 2:00 AM to 10:00 AM, during peak migration flight times for three simultaneous nights throughout the first 5 weeks of spring migration (17 May- 26 June). I set the ARU to record 10 minutes of bird songs at the end of every hour, designing the sounds to pause during the respective 10 minutes. I also deployed four additional ARUs approximately half a mile in from the speaker unit in four cardinal directions to measure baseline songbird densities. Bird abundance was determined by counting the number of detected bird songs within the 8 unique, 10-minute recordings. The efficacy of the two respective acoustic signals was estimated by comparing the number of birds detected at each site to the number of birds detected at the ecologically similar control site.

3.2.4 Predator and Synthetic Deterrent: Fall 2023

To determine whether the sound signals established in my spring experiment were effective at reducing songbird collisions within urban settings I deployed two deterrents at buildings in Chicago that have records of past bird collisions with acoustic deterrents during the fall 2023 migration window (Figure 1, 2). Specifically, two deterrents were deployed at the Kellogg Global Hub and the R Athletic Center, located on Northwestern University’s Evanston campus. Deterrents were placed along a vegetated strip to the East of the Ryan Athletic Center and the remaining deterrents were placed adjacent to Hutcheson Field to the East of the Kellogg Global hub building. The deterrent at the

Ryan Athletic Center was programmed to play the biological predator call, whereas the deterrent at the Kellogg Global Hub was programmed to play the synthetic, broadband white noise (2-10kHz), first developed in my Spring 2023 experiment.

Figure 1. Photograph of the Kellogg Global Hub, a building on Northwestern University’s campus that has reported historically large numbers of bird collisions. I deployed one of the speaker units in the green space directly in front of the building.

Figure 2. Photograph of a deterrent unit where it was deployed in the greenspace in front of the Ryan Athletic Center, a building on Northwestern University's campus that has reported historically large numbers of bird collisions. Notably, the building has large installments of glass-paned windows, and is located directly on the shore of Lake Michigan.

3.2.5 Statistical Analysis

For the fall preliminary experiment, wherein I conducted mist net surveys, I calculated bird capture rates per sampling day by dividing the number of birds captured by the total mist net hours which accounts for both time and number of operating nets. To determine the effect of sound treatment on capture rates I conducted a two-way ANOVA test in the R-analysis base R package with the function "aov" (R Development Core Team 2022). Acoustic treatment (control, attractant, deterrent) and study site (nara, slough) were included as explanatory variables. To account for random variation associated with fluctuating migration numbers each day, I included date as a random offset. I also conducted post-hoc analyses on both acoustic treatment and study site using the "TukeyHSD" function (R Development Core Team 2022).

For my ARU experiment the following spring season, I identified and sorted sound recordings from each ARU using the RavenPro 1.6 software (Cornell Lab of Ornithology). To determine the effect of sound treatment on detection rates I conducted one-way ANOVA tests on detections from each respective site in the R-analysis base R package with function “aov” (R Development Core Team 2022). Acoustic treatment (synthetic, predator, control) was included as the explanatory variable. To distinguish the effect of each unique acoustic treatment I also conducted post-hoc analyses using the “TukeyHSD” function in the base R package (R Development Core Team 2022). For reference regarding relevance to migratory birds, I removed all detections from non-migratory species and reran both the ANOVA and Tukey test on detections from the experimental ARU site. To compare control site detections trends to experimental detections across sampling time, I combined paired control site datasets and fit linear regressions to the resulting control groups (Control Group 1 & Control Group 2) and the experimental data set using the “lm” function in the “dplyr” R package (Wickham et al., 2023).

Collision data from the Chicago deployment was collected by the Chicago Bird Collision Monitors, a small non-profit, and was not made available to me before writing this chapter, and thus was not included in statistical analyses.

3.3 Results

3.3.1 Preliminary Deterrent: Fall 2022

I analyzed capture rates from a total of 34 sampling observations representing two experimental locations (nara, slough), each site had 17 sampling efforts on simultaneous days. When accounting for random variation in migratory number fluctuations, the interaction between treatment and site had a significant effect on capture rate (ANOVA $F_{2,1} = 6.908$, P = 0.003). Specifically, treatment had the most significant effect. Post hoc comparisons between acoustic treatments suggested the attractant had the most significant effect resulting in an average of 37 more captures per 100 mist net hours relative to the control treatment (p-value = 0.003) (Figure 3). Post hoc comparison also revealed significant disparity in capture rate between study sites, the slough site resulting in an average of 18 less captures per 100 mist net hours relative to the nara site (p-value = 0.040).

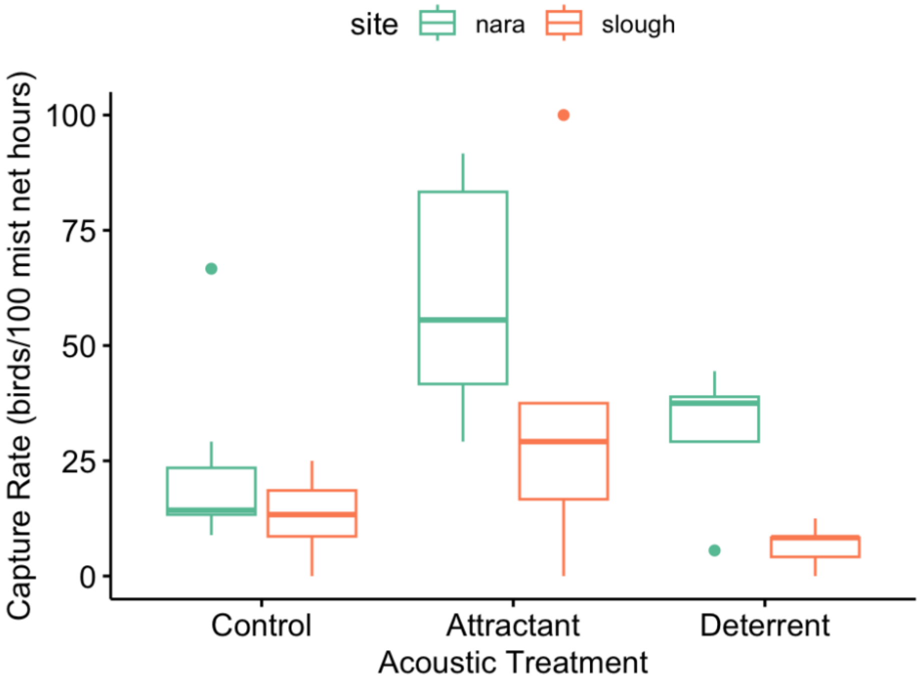


Figure 3. Boxplot depicting total capture rate of birds by sample site (nara = green, slough = red) and acoustic treatment (control, attractant, deterrent). Total sample size was 34 days, representing 17 paired days. Data reflects mist-net capture rates at study sites from two locations along the Portage Canal, a body of water located in the Keweenaw Peninsula of the Upper Peninsula of Michigan. Data was collected from August 18, 2022 to September 17, 2022.

3.3.2 Experimental Design: Spring 2023

I analyzed a total of 2,581 avian detections from a total of 42 days across 5 different sites. 50 unique bird species were detected, 38 of which were migratory species, the most common species being Blue-headed Vireo (*Vireo solitarius*), Blackburnian Warbler (*Setophaga fusca*), Chestnut-sided Warbler (*Setophaga pensylvanica*) and Nashville Warbler (*Leiothlypis ruficapilla*). Analysis of the total detections from the experimental site suggested that acoustic treatment had a significant effect on detection rate (ANOVA $F_{2,38} = 16.76$, $P < 0.001$). When the detections were filtered to include only migratory species, acoustic treatment had a more pronounced effect on detection rate (ANOVA $F_{2,38} = 24.88$, $P < 0.001$) (Figure 4).

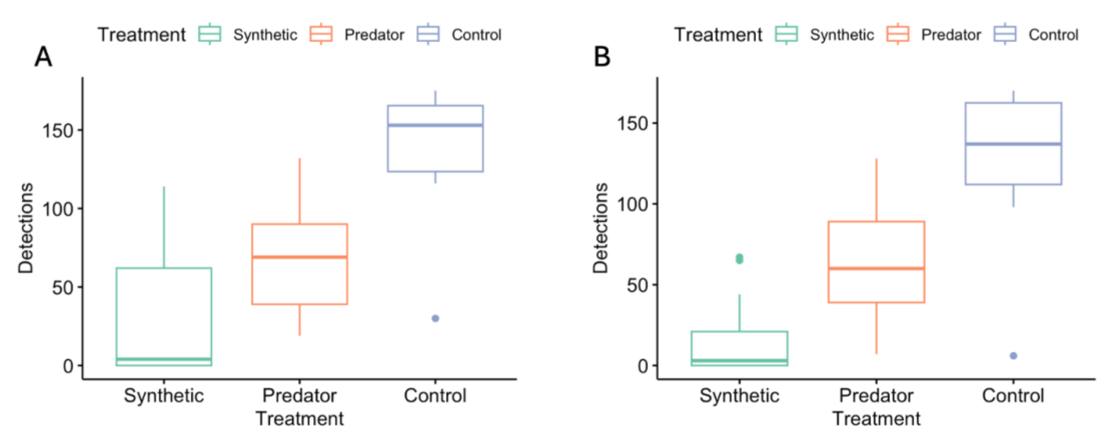


Figure 4. Effect of acoustic treatment (synthetic, predator, control) on bird detection rate at the experimental site including all detections (A) and including just migratory species detections (B). Detections were obtained from automatic recording units deployed from May 18 to June 26, 2024. The synthetic and predator acoustic treatments were each broadcast at the experimental site for 15 days, respectively. The site was monitored following termination of acoustic treatments for 6 more days as a control proxy. Treatment effect on detections; A) (ANOVA $F_{2,38} = 16.76$, $P < 0.001$); B) (ANOVA $F_{2,38} = 24.88$, $P < 0.001$).

Conversely, analysis of the total detections from the four control sites revealed either non-significant or contrasting effects of acoustic treatment days on detection rates, wherein detections decreased on days when the control treatment was applied to the experimental site (Figure 5). Given that no acoustic treatment was applied to the four control sites, detection numbers reflect background bird abundances adjacent to the experimental site, suggesting the abundance was either stable or increasing with progressive sampling days. As acoustic treatment effects at the experimental site were antithetical to trends within the control data, my results suggest that acoustic treatment effectively decreased bird detection rates despite otherwise contradicting baseline bird abundances.

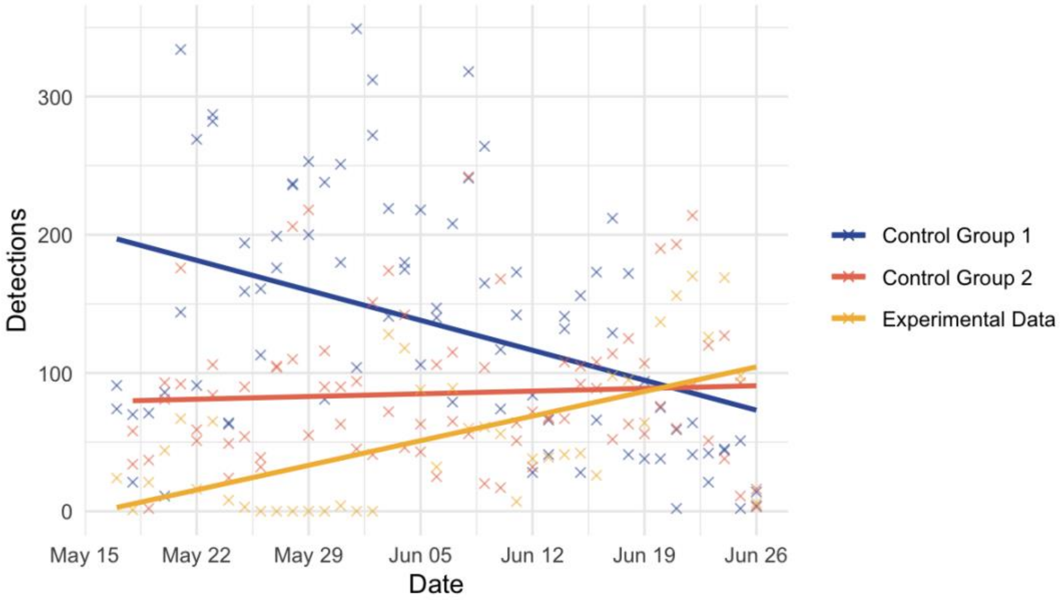


Figure 5. Regression trendlines representing avian detections throughout time across control groups relative to the experimental site. Each control group represents a paired control site, wherein data from each site was combined to create one control group. The experimental data represents one site wherein the acoustic treatment was applied. At the experimental site, the synthetic acoustic treatment was broadcast from May 17 to June 02, the predator acoustic treatment was broadcast from June 03 to June 19 and a period of no sound (control) was monitored from June 20 to June 26. Control Group 1 (slope = -3.097, $p < 0.001$), Control Group 2 (slope = 0.278, $p = 0.589$), Experimental Data (slope = 2.542, $p < 0.001$).

3.4 Discussion

Avian populations, particularly migratory species, have experienced drastic declines due to collisions with anthropogenic structures, such as skyscrapers (Klem, Jr. D 2008; Loss et al, 2014). Given the continued sprawl of urbanization, collision mortalities threaten the vitality of North America's bird species, many of which are already at risk of extinction from myriad of additional anthropogenic threats (Xu et al. 2020). However, the profound scale of avian mortality from collisions provides opportunity to enact powerful conservation actions that could potentially result in solutions that directly bolster bird populations. Nevertheless, bird-building collisions remain enigmatic, having a multitude of interrelated drivers including both environmental and evolutionary factors (Elmore et al., 2020; Hager et al., 2017; Loss et al., 2014; Loss et al., 2019; Ocampo-Peñuela et al., 2016), thus deriving a feasible solution has proven to be challenging. My study adds to the understanding of the social mechanisms behind collisions as well as provides evidence for a novel direction from which to mitigate collision mortalities via manipulated acoustic signals.

Results from my preliminary experiment suggest that favorable acoustic signals from conspecifics can bolster local abundances and drive flight decisions (Figure 1). Similar findings have been observed in other studies, offering evidence that migratory birds may use the presence of conspecific songs as a marker of high-quality stopover habitat. For instance, Mukhin et al 2008, detected significantly more Eurasian reed warblers (*Acrocephalus scirpaceus)* following nights of conspecific playbacks. Likewise, De La Hera et al 2017, found capture rates of Bluethroats (*Luscinia svecica*) to be associated with heterospecific playback. Acoustic cues may allow migrating birds to locate advantageous rest and refueling areas without directly sampling the habitat and potentially wasting energetic resources or being exposed to predators (Mukhin et al., 2008; Szymkowiak et al., 2017). Acoustic projection of relevant species songs likely encourages birds, near acoustic signals, to select habitats they otherwise would not settle. Response to interspecific acoustic cues has been integrated into recent conservation strategies, wherein acoustic playbacks have been successfully deployed as attractants at recently restored sites (Molles et al., 2008).

In my second field experiment, the significant decrease in local bird abundance observed during the duration of the acoustic deterrent suggests that manipulated soundscapes may be effective at dissuading migratory birds from entering a given area. While both the predator call track and 2-10 kHZ frequency broadband sound was associated with significant decreases in bird relative abundance, the 2-10 kHZ broadband acoustic track was particularly effective, reporting the greatest diversion from baseline bird densities. Similar success has been reported by several other studies, in particular, Boycott et al (2018) found decreased local bird densities when a 4-6 kHz acoustic signal was projected into the surrounding airspace. Additionally, approaching birds were more likely to deaccelerate and change flight heading upon detection of the acoustic signal (Boycott et al., 2018). Likewise, Swaddle et al (2015) applied a comparable broadband acoustic sound to an airfield and found significant avian abundance decreases even after individuals may have become habituated to the sound. This is in contrast to previous studies wherein predator alarm calls effectuated immediate avoidance behavior but did not remain efficacious over an extended period of time (Rivadeneira et al., 2018). This highlights the importance of using communication-masking sounds in place of acute, startle-inducing sounds when developing collision deterrents, which may potentially extend the effectiveness of the acoustic deterrent.

This may be attributed to critical function vocal communication has in the coordination of migratory bird’s flight paths (Farnsworth & Lovette, 2008; Gayk et al., 2021; Hamilton W.J., 1962; Mukhin et al., 2008; Szymkowiak et al., 2017; Winger et al., 2019). In particular, some migratory bird species emit distinct, high-frequency calls when migrating, including those species that collide with buildings at disproportionally high rates (Winger et al., 2019). Several studies suggest that these calls, known as flight calls, may serve as a critical medium of informational exchange between flock members and potentially between various flocks (Farnsworth A., 2005; Gayk Z.G & D.J. Mennill, 2023; Hamilton W.J., 1962; Smith et al 2014). My results suggest that by over-saturating the local soundscape with a disruptive sound, critical communication networks are broken down, effectively forcing migratory birds to avoid the given area in order to preserve flock coordination (Thady et al., 2022). The efficacy of the synthetic deterrent is made further effective by the deterrent's capacity to decrease bird detections despite fluctuating background bird abundance across the local landscape.

Conjointly, my results suggest that acoustic signals can be developed to manipulate migratory species flight paths in natural systems. Specifically, a disruptive, high-frequency sound that masks communication may be strategically deployed to deter migratory birds from entering airspace in proximity to high-risk anthropogenic structures or urban perimeters. Moreover, the deployment of a sound interspersed with common species songs may be used to artificially increase migratory bird abundance within favorable habitats. Used in tandem, developed acoustic cues may have the profound capacity to guide migratory birds away from dangerous buildings and shepard them to safer or higher quality stopover habitats.

While most research does not have the opportunity to apply their findings to actual conservation circumstances or enact direct change, I had the exciting opportunity to deploy the acoustic deterrents on two historically high-risk buildings near Chicago, Illinois, in a preliminary trial study. While I am still awaiting mortality results from the experiment, I believe it is important to highlight the applicability of my findings in the search for real-world solutions to the devastating impact of bird-building collisions. Importantly, my field results informed conservation action, in collaboration with the volunteer network: Chicago Bird Collision Monitors, as well as the Northwestern University community. There is continued collaboration with the Student Government Sustainability Committee to further develop an effective mitigation solution, with the potential option to employ speakers as well as use the existing network of bird-safe glass window treatments. If successful, this approach may be adopted by building managers more broadly.

However, given the complex and enigmatic mechanisms behind bird-building collisions, uniform success across environments and local circumstances may be difficult to predict. In particular, the function of stopover (Linscott & Senner, 2021), may impact the way migratory birds respond to acoustic stimuli. For example, my field studies were conducted in expansively rural locations wherein birds’ movements and concurrent communicative dynamics may be altered relative to a highly urbanized location along the leading front of a large body of water. Such dissimilar locations likely reflect dissimilar ways birds use stopover (Linscott & Senner, 2021; Schmaljohann et al., 2022), whereby small patches of habitat within urban landscapes may serve as an island of critical habitat. Given the potential importance of these patches of habitat, understanding the unforeseen effects of an acoustic deterrent on birds using such locations represents an important next step.

Additional obstacles in acoustic signal deployment within urban environments should be considered as well. For instance, sound behaves differently in various substrates and thus emits dissimilar acoustic properties depending on the surrounding environment. Such subtleties may affect birds' responses due to their heightened sensitivity to urban soundscape changes (Cardoso, G. C., 2014; McClure et al., 2013). Moreover, people may likely not tolerate the most effective deterrent. Given that migratory birds' hearing sensitivity is closely aligned with humans (Gill, F. B., 2007), acoustic signals developed for birds are also detectable by humans. Thus, continued and creative adaptations to the timing, duration and placement of such acoustic speakers may need to be developed to facilitate their long-term deployment in urban environments.

My research highlights the potential importance of acoustic sensory ecology and communicative behaviors in the mitigation of bird-building collisions. Future research should address specific drivers of collisions and the role flock-communication may play in collision rates.

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4.3 Chapter Three

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