ABSTRACT

| | |
|---|---|
| Title of Dissertation: | MOVING THE GOALPOSTS: MIGRATORY BIRDS IN A CHANGING WORLD |
| | Claire Elizabeth Nemes, Doctor of Philosophy, 2023 |
| Dissertation directed by: | Assistant Professor Emily B. Cohen - Marine, Estuarine, and Environmental Science (MEES) |

Billions of birds undertake migratory movements each year, traveling distances that range from several hundreds to tens of thousands of kilometers. Migratory birds must be flexible enough to cope with the fluctuating conditions they encounter during these journeys and at their destinations. However, humans are rapidly and dramatically changing the environment across all portions of migratory species' ranges through habitat destruction and conversion, introduction of invasive species, climate change, and other alterations. My dissertation research seeks to understand the constraints and threats facing birds during two understudied phases of the annual cycle: migration and the non-breeding stationary period. In **Chapter 1**, I explore how human activities may nonlethally affect birds during migration. I reviewed the scientific literature for evidence of nonlethal effects and of interacting threats that may compound fitness costs to migrating birds. In general, I found that scientific understanding of nonlethal effects during migration lags behind research on direct mortality. Because birds migrate through increasingly anthropogenic landscapes and airspaces, I identify this knowledge gap as a hindrance to effective

conservation of migratory birds. In **Chapter 2**, I investigate if individual songbirds adjust the rate and timing of spring migration based on the vegetation phenology they encounter within North America which may allow them to keep pace with advancing spring phenology under climate change. In the spring, migrating birds must quickly reach their breeding grounds to secure territories and mates ahead of the competition, but individuals that arrive too early may encounter inclement weather or food shortages. Using the Motus automated radio telemetry network, I tracked individual songbirds as they traveled from the southern U.S. towards their breeding areas in spring. I used estimates of spring onset timing at different points on their migration routes to determine if birds traveled in sync with the "green wave" of emerging vegetation or if they used a different strategy. I found that birds migrating from their non-breeding areas arrived in the southern U.S. well after local spring onset, but were able to catch up to the wave of emerging spring vegetation as they traveled northwards, following a "catching up" strategy rather than a "surfing" one. In **Chapter 3**, I examine how individual songbirds respond to the threat of predation during migratory stopover, when they must balance conflicting demands of refueling and avoiding predators. Migrating birds must contend with both native avian predators such as hawks (*Accipiter sp.*) and abundant introduced predators such as free-roaming domestic cats (*Felis catus*), yet their behavioral responses to cats have been little studied during migration. Using an aviary experiment, I exposed wild Gray Catbirds *Dumetella carolinensis* to either a hawk or a domestic cat and observed their behaviors before and after exposure to determine if they responded appropriately to the threat posed by each predator. When compared with a control group, Catbirds responded differently to both types of predators in the short term, but I detected no differences in their behavior after release. This study provides novel insights into the possible nonlethal effects of introduced predators that birds may

encounter during migration. In **Chapter 4**, I shift focus to explore the threat that free-roaming domestic cats pose to birds in the Caribbean within a Neotropical city. Urban regions are increasingly recognized to provide valuable wildlife habitat but may also contain hazards such as introduced predators, and we currently lack information on the effects of free-roaming cats on migratory and resident bird species during non-breeding seasons. I designed a camera trapping project in San Juan, Puerto Rico to estimate free-roaming cat densities across a gradient of urbanization as a step towards understanding their potential impacts on wildlife. I deployed cameras across 16 trapping grids at three levels of urbanization and used photographic captures of cats to build spatial capture-recapture models. Estimated cat densities ranged from 48 ± 8 (SE) cats/km$^2$ in exurban areas to 473 ± 40 cats/km$^2$ in the most heavily urbanized parts of the city. These data may prove useful for conservation practitioners in San Juan deciding where to target cat management efforts for the benefit of urban wildlife and public health.

# MOVING THE GOALPOSTS: MIGRATORY BIRDS IN A CHANGING WORLD

by

Claire Elizabeth Nemes

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2023

Advisory Committee:
Assistant Professor Emily B. Cohen, Chair
Professor Matthew C. Fitzpatrick
Assistant Professor Jennifer M. Mullinax
D.T. Tyler Flockhart, Ph.D.
Associate Professor Colin E. Studds
Professor William F. Fagan, Dean's Representative

# Dedication

This one is for the birds.

# Acknowledgements

Almost as soon as I embarked on my Ph.D., I was excited to start a list of the people to thank in my dissertation. Every time I've opened the document to add new entries over the years, it has reminded me that while a dissertation can feel like a lonely endeavor, I've had the support and guidance of so many people along the way. This is a list of their kindnesses.

First, thank you to the members of my dissertation committee. I could not have asked for a better advisor than Dr. Emily Cohen. She took a risk in adopting me as her first Ph.D. student and though I have not always made it easy, she has been unflaggingly supportive and patient through pandemic pivots, fieldwork cancellations, and various mishaps and triumphs. From her I have learned the importance of telling a story with your science (and getting to the damn point), developing collaborations, leaning on your friends, and celebrating each victory, preferably with good beer. There has been no better scientist with whom to learn about the complexity and beauty of animal migration. Matt Fitzpatrick also took a chance on me and I am grateful for his thoughtful advice, open-door policy, and for not rolling his eyes too hard at the endless bird hype. I know the one thing he most hoped to teach me was how to like Tool, and I'm sorry to have disappointed. Tyler Flockhart is the one who got this whole party started, and I'm grateful for the many deep, thought-provoking discussions about not only about the science but the psychology, sociology, and ethics of free-roaming cats. I'm thankful that Jennifer Mullinax has been in my corner all the way from undergrad, through my M.S., and now during my PhD. Colin Studds has provided helpful questions on my research through the years.

Thank you to the members of the Animal Migration Research Group: Megan Massa, Sergio Cabrera-Cruz, Joely DeSimone, Meredith Anderson, and Luke DeGroote. It has been a joy to study the wonders of migration with you all and I'm grateful for all the birding adventures,

interesting discussions, and interventions when I couldn't get my words or my R code to work. I'm grateful to the small but mighty AL graduate student body; a special shout out to Joel Bostic, Annie Carew, Megan Massa, and Juliet Nagel. The entire Appalachian Lab community has been incredibly helpful, particularly Barb Jenkins, Kristen Harper, Cami Martin, John Piasecki, Deb Richards, and Rhonda Schwinabart. Special thanks to Heather Johnson, keeper of knowledge and dispatcher of nonsense, for being an unfailing advocate for students. I am also grateful to Dave Nelson, Cat Davis, and other members of the AL DEI group; to Steven Guinn and Andrew Elmore for their remote sensing wisdom; and to all of the AL staff and faculty who I've pestered with questions. Thank you to the many staff, faculty, and students at UMCES and MEES, especially to Amy Griffin for her never-ending positivity and helpfulness, and to the members of the UMCES Diversity, Equity, and Inclusion Collaborative and the Graduate Student Council.

This research was made possible through the generosity and friendship of the staff and volunteers at Powdermill Avian Research Center, especially Annie Lindsay, Mary Shidel, and Luke DeGroote. I am grateful to my colleagues in Puerto Rico, especially Emilio Font Nicole and Gisela Crespo Martinez, for their wisdom, insights, and help in the field. My dissertation would not have been possible without the financial support of UMCES, UMD, and the MEES program, including AL Student Research Project and Travel Awards, MEES Graduate Student Summer Research Fellowship, the Reed Evans Menzer Memorial Graduate Award, Dean's Fellowship, and the Fall Semester Fellowship for Students Delayed by Covid-19. Additional research and travel funds were provided by the American Philosophical Society Lewis and Clark Fund for Exploration and Field Research, the ABC Humane Wildlife Foundation, the Florida Ornithological Society, the Nuttall Ornithological Society, the AEHS Foundation, and the American Ornithological Society.

I am grateful for the support of a wonderful network of friends, old and new. Special thanks to Larry and Ellen Moon, who have truly become like family, for the continuing education in farm life, news from the woods and field, sharing the love of your land, and letting me run wild in ways that kept me sane during grad school and the pandemic.

Last but not least, thank you to my family: my dad Kurt Nemes, stepmom Laura Zam, mom Judy Barnes, stepdad Bob Barnes, and brilliant sister Simone Nemes. Somehow I had the great fortune to be born into a family of exceptionally funny, passionate, and creative weirdos who instilled in me a love of learning and a curiosity about the world, and who have always supported my critter obsessions and often-winding academic path. And to my four-legged family members, Odin, Acorn, Stranger, and Veery, for moral and thermal support. I love you all.

These and so many others have helped along the way, whether they know it or not. It has been a privilege to learn about this beautiful world from and with you all.

# Table of Contents

# List of Tables

## Chapter 2

Chapter 3



Chapter 4

# List of Figures

## Chapter 1



## Chapter 2

## Chapter 3

Chapter 4

# Chapter 1: More than mortality: Nonlethal anthropogenic threats impact success and fitness of migrating birds

**Chapter Note:** This chapter is in revision for the journal *Ornithological Applications* with co-authors Sergio A. Cabrera-Cruz, Meredith Anderson, Lucas W. DeGroote, Joely G. DeSimone, Megan Massa, and Emily B. Cohen.


## Abstract

Migrating birds must contend with an increasing array of anthropogenic threats including artificial light, structures, introduced species, and pollutants. These and other anthropogenic hazards that birds encounter *en route* cause mortality but can also negatively affect migrants' condition and timing. These nonlethal effects of anthropogenic threats are harder to measure and therefore less well understood than mortality, yet have the potential to contribute to population declines. For example, migrating birds frequently die after colliding with buildings and other structures, but collisions can also affect migrating birds nonlethally if injuries impair an individual's ability to fly, refuel, or successfully navigate to the destination on time. Though not immediately fatal, such injuries can ultimately lead to reduced reproductive success or future survival. Interactions among threat types may compound both lethal and nonlethal effects. For instance, anthropogenic light pollution attracts and disorients migrants, increasing the likelihood of window strikes, and birds stunned or injured by collisions are more vulnerable to introduced predators. Here, we review current knowledge of the nonlethal effects of anthropogenic threats during migration and the pathways through which they exert fitness costs. We also describe ways that threats may interact to exacerbate effects on migrating birds. In doing so, we identify

knowledge gaps and suggest areas for future research to better understand *en route* nonlethal threats. We suggest that in the absence of more information, managing specific threat sources that interact with a greater number of other anthropogenic threats may yield the largest conservation benefit. While mortality from anthropogenic sources has received attention as a key driver of population declines, an accurate measure of the impacts of human activity on migrating birds must include the cumulative and interacting effects of nonlethal threats that extend beyond immediate mortality *en route* to influence overall migration success and lifetime fitness.

## Introduction

Migration is the most dangerous period of the annual cycle for adult migratory birds (Sillett and Holmes 2002a, Klaassen et al. 2014, Rockwell et al. 2017a, Paxton et al. 2017). During journeys that may span months and cross continents, birds navigate unfamiliar and variable conditions in terrestrial, marine, and aerial environments. Migratory birds are well-adapted to overcome the challenges of migration (Moore 2018) but anthropogenic activities have increasingly modified the environments birds encounter *en route*, especially in the decades since the advent of the industrial revolution (Davis 1955). Urbanization, the most drastic transformation to the landscape, is mostly concentrated in mid-temperate latitudes around the world, south of regions that harbor the greatest richness of breeding migratory bird species (Seto et al. 2011, Somveille et al. 2013, Zhou et al. 2015). Thus, regions traversed by migrating birds are increasingly sown with evolutionarily novel threats that can impose considerable costs on bird fitness (Lambertucci et al. 2015, Cabrera-Cruz et al. 2018a, La Sorte et al. 2022). These changes may be inflating the costs of being a migratory animal (Wilcove and Wikelski 2008, Hardesty-Moore et al. 2018).

Research on anthropogenic threats to birds has frequently focused on **direct mortality sources**, defined as hazards such as window collisions and cat predation that are "characterized by relative clarity of cause and effect" (Loss et al. 2015a). Other anthropogenic factors such as climate change are considered **indirect mortality sources** because they kill birds via intermediate mechanisms (Loss et al. 2012, Calvert et al. 2013b, Loss et al. 2015a). Both direct and indirect anthropogenic mortality sources can also produce nonlethal effects or "delayed fitness costs" that reduce an individual's survival probability or reproductive output (Klaassen et al. 2012, Schmaljohann et al. 2022). Threat effects may not always materialize at the source and are likely increasing the costs of migration in ways that are typically unaccounted for in

estimates of "direct mortality." Despite their potential importance, the nonlethal effects of anthropogenic threats during migration have only recently begun to receive research attention (e.g., Ware et al. 2015, Seewagen 2020, Overton et al. 2022).

Although threats are often studied in isolation, they can interact with one another to produce synergistic effects (Dutta 2017, Mahon et al. 2019, Norris et al. 2021, Richard et al. 2021), which may be lethal or nonlethal (Kummer et al. 2016, Winger et al. 2019b, Van Doren et al. 2021, Rebolo-Ifrán et al. 2021). Synergistic effects of multiple anthropogenic threats during migratory periods remain understudied (Dutta 2017, Richard et al. 2021). However, the repetition, combination, and interaction of even seemingly minor threats can substantially increase the extinction risk of wildlife populations (Kimmel et al. 2022), demonstrating that these effects must not be overlooked. A narrow focus on direct mortality of migrating birds due to anthropogenic threats, ignoring nonlethal threats and interactions, substantially underestimates the total cost of human activity on migrating birds. In this review we briefly describe **lethal effects** (i.e., mortality) of eight anthropogenic threat types before discussing their **nonlethal effects** on migrating birds (Box 1). We first identify the primary pathways through which anthropogenic threats during

**Box 1.** Glossary

**Anthropogenic threats:** Physical or sensory elements added to the environment, either intentionally by humans or unintentionally as a byproduct of human activity, that impose fitness costs on migrating birds.

**Fitness costs:** Increased mortality, reductions in reproductive success, and/or reductions in future survival probability.

**Lethal effects:** Effects of anthropogenic threats that cause immediate or delayed mortality.

**Nonlethal effects:** Effects of anthropogenic threats that cause a reduction in future reproductive output or survival probability, or that increase susceptibility to the effects of other threats through one or more intermediate mechanisms.

**Interacting effects:** Anthropogenic threats that interact with one another to produce either lethal or nonlethal effects; these may be additive or synergistic.

migration can cause nonlethal fitness costs. These include effects on a migrant's (1) **physiological condition** or health, (2) **timing** of migration, (3) **orientation and navigation** ability, and (4) migration **route** (Figure 1). We briefly describe each anthropogenic threat and its lethal effects, both immediate and delayed, before summarizing the current knowledge of the threat's nonlethal effects on migrating birds. We mainly consider threats to birds migrating through terrestrial (rather than marine) environments. In cases where nonlethal effects have only been documented during non-migration phases of the annual cycle or in non-migratory taxa, we draw from that literature to hypothesize potential impacts on migrating birds (as in Seewagen 2020). Next, we identify evidence for cumulative and synergistic effects and explore the mechanisms through which multiple threats interact to harm migrating birds. Finally, we highlight knowledge gaps and discuss the conservation implications and potential pitfalls of failing to consider other consequences of human activity on migrating birds beyond direct mortality.

## Anthropogenic Threat Pathways Leading to Fitness Costs

We identified four pathways through which factors during migration influence bird fitness. The anthropogenic threats that migrating birds encounter *en route* can have lethal fitness costs (i.e., mortality) or nonlethal fitness costs that reduce reproductive success or survival during a future stage of the annual cycle (Senner et al. 2015) (Figure 2). These costs are incurred through four non-mutually exclusive pathways that we describe here. An example diagram of the pathways through which a single threat can affect fitness is shown in Figure 1.

**Physiological Condition:** We use "condition" to indicate both fuel stores (fat) and other components of health and vitality (Klaassen et al. 2012). Upon arrival at their destination, migrants must forage, avoid predators and competitors, and/or find mates. Their health and

energetic condition at the end of the journey also influences subsequent survival and reproduction (Klaassen et al. 2012, Halupka et al. 2017, Moore 2018). Nonlethal threats can change a bird's condition by reducing its energy stores through an impaired ability or motivation to forage (Jenni and Schaub 2003a); by causing injury, illness, or exhaustion (Van Doren et al. 2017, Linscott and Senner 2021); or by increasing disturbance and stress (Le Corre et al. 2009). Threats that reduce physiological condition, particularly fat stores, pose a potential fitness cost by delaying migration timing (Seewagen and Guglielmo 2010) or hampering reproductive ability upon arrival to breeding areas (Sandberg and Moore 1996).

**Migration Timing:** Appropriate timing of arrival to breeding, stopover, and wintering sites is critical for migratory birds to secure high-quality territories and mates, maximize reproductive potential, secure food resources for refueling, and avoid adverse weather (Sandberg and Moore 1996, Kokko 1999, Jenni and Schaub 2003a, Smith and Moore 2005a, Schmaljohann and Both 2017). Delays may arise via changes to a bird's physical condition, but also through changes to its route, environmental cues that trigger departure, suitable flight conditions, and other factors (Jenni and Schaub 2003a, Åkesson and Helm 2020). Any *en route* conditions that delay a migrant's arrival to the breeding area in spring may hinder its chances of maximizing its reproductive potential (Sandberg and Moore 1996, Smith and Moore 2005a, Costa et al. 2021). Delayed arrival to the non-breeding area can result in lower-quality habitat for territorial species, delaying spring migration departure (Studds and Marra 2007, Cooper et al. 2015, but see González et al. 2020), though arrival timing in wintering areas is generally poorly understood (Kobori et al. 2012). The timing of arrival to stopover sites is also important because both the needs of a migrating bird and the ability of stopover sites to meet those needs can vary within a season (Schaub and Jenni 2000, Linscott and Senner 2021, Cohen et al. 2022b, Schmaljohann et

al. 2022). Thus, proper timing relative to external conditions is critical to a bird migration's success, and any threat-related changes to the migration schedule that a bird would not have experienced otherwise (typically delays) pose a potential fitness cost.

**Orientation and Navigation:** Migratory birds use an internal clock and compass mechanism coupled with a variety of external cues, including the Earth's magnetic field, polarized light, and the position of celestial bodies, to orient themselves and navigate to their destination (Alerstam et al. 2003, Åkesson and Hedenström 2007, Åkesson and Helm 2020). Although birds' navigation ability is remarkably flexible in the face of changing *en route* conditions (Åkesson and Helm 2020), anthropogenic threats can interfere with a bird's ability to correctly perceive or interpret environmental cues used for orientation and navigation. Disoriented migrants may deplete their energy reserves in flight (Ronconi et al. 2015), imposing fitness costs through reduced condition, delayed timing, or failure to reach the destination.

**Migration Route:** Migrating birds are expected to follow routes that minimize overall time, energy, or predation risk over the course of the journey (Alerstam and Lindström 1990, Alerstam 2001). Anthropogenic changes to the physical and sensory environment may cause migrating birds to alter or adjust their route, move to alternative stopover sites, or change their stopover frequency. Threat-related changes to the route presumably lengthens the duration of migration (i.e., timing) and can affect condition via increased energy expenditure or the opportunity costs of using lower-quality stopover or airspace habitat, potentially leading to costly delays (Alerstam 2001, Overton et al. 2022).

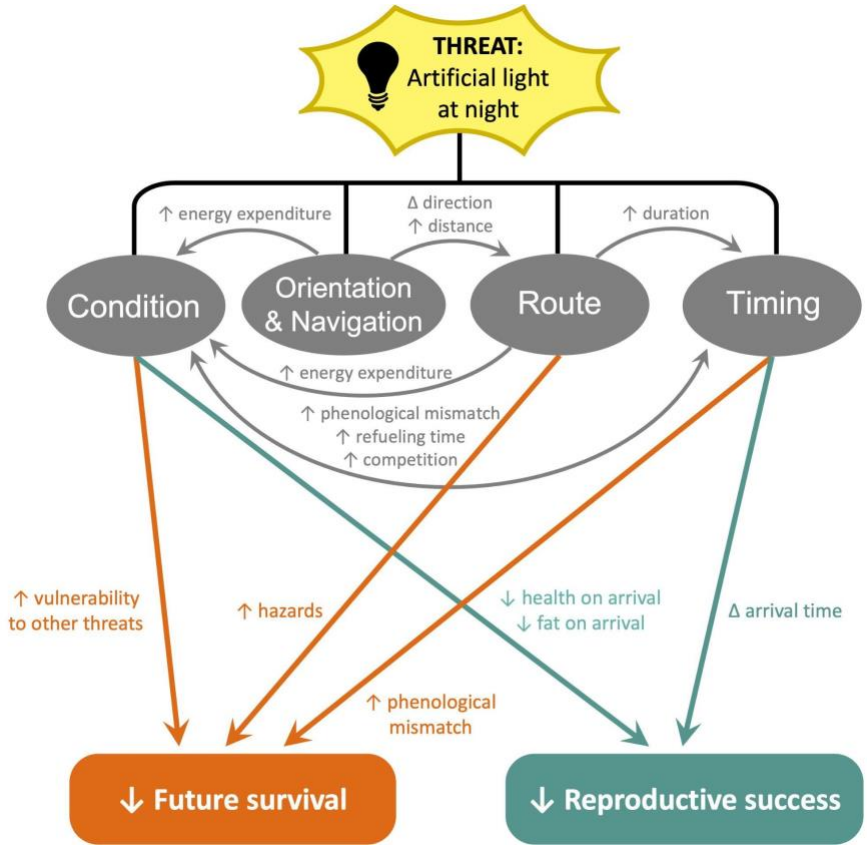


**Figure 1.** Conceptual diagram of the pathways through which a single anthropogenic threat, artificial light at night (yellow starburst) can influence the two components of a successful migration: **future survival** and **reproductive success** across the annual cycle (rounded boxes). Threats affect reproductive success and / or survival through intermediate pathways (purple ovals): by changing a migrant's physical **condition**, **orientation and navigation**, **route**, or **migration timing**. Gray arrows are labeled with how linkages between pathways can occur: for example, artificial light at night attracts birds in flight (affecting orientation), which causes them to change direction and lengthen the distance traveled (affecting route), which leads to increased energy expenditure in flight (affecting condition). Colored arrows are labeled with the ways that artificial light at night can ultimately decrease survival probability (orange) and reproductive success (teal) via the four pathways.

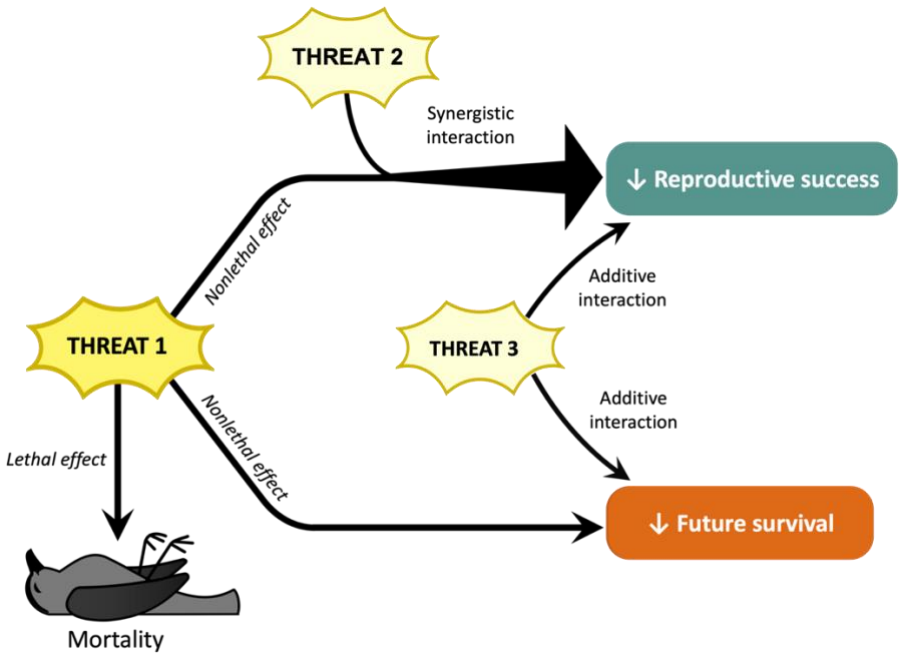


**Figure 2.** Anthropogenic threats (yellow starbursts) can affect migrating birds either individually or in combination with other threat sources. **Lethal effects** result in either immediate or delayed mortality. **Nonlethal effects** can reduce reproductive success or future survival probability (rounded boxes). Migrants can experience multiple threats *en route* that influence reproduction or survival independently of one another (**additive interaction**) or that interact to have a greater impact on reproduction and / or survival than they would in isolation (**synergistic interaction**).

## Anthropogenic Threat Types

In the sections below, we review the effects of eight types of anthropogenic threats to migrating birds, whose lethal effects we briefly describe before discussing their supported and hypothesized nonlethal effects through the pathways described above. In the final section, we discuss interactive effects of these threats. We included anthropogenic threats that represent some of the largest sources of annual bird mortality, following descriptions elsewhere (e.g., Calvert et al. 2013, Loss et al. 2015, Richard et al. 2021). These include (1) human-made structures (buildings, wind turbines, powerlines, etc.), which are considered to be the primary sources of collision mortality during migration; two human-produced sensory pollutants: (2) artificial light at night (ALAN) and (3) noise pollution; (4) environmental contaminants

(focusing on agricultural chemicals and heavy metals); and (5) free-roaming domestic cats (*Felis catus*). We also included two additional threats caused or exacerbated by humans that are not typically considered to cause large-scale direct mortality but may nonetheless threaten migrating birds: (6) introduced plants and (7) wildfires. In addition, we consider the overarching effects of (8) anthropogenic climate change on bird migration. Increasing wildfire activity is one of many consequences of climate change, but we chose to discuss these threats separately due to their different pathways and effects on fitness. While hunting and trapping is a major threat to migrating birds globally, particularly in the East Asian-Australasian and Afro-Palearctic migration systems (Vickery et al. 2014, Yong et al. 2015, Khelifa et al. 2017, Brochet et al. 2019, Buchan et al. 2022, Lees et al. 2022), we did not find sufficient evidence of nonlethal effects of hunting during migration to include it in this review. We only briefly address stressors that are a consequence of the removal of elements from the landscape (e.g., habitat loss and fragmentation), though the importance of these factors in bird population declines cannot be understated. Relatedly, we demonstrate how many of these anthropogenic threats can cause functional habitat degradation, effectively reducing the availability of otherwise high quality or protected airspace and stopover habitats (e.g., Ware et al. 2015). It is possible that this synthesis will lead to discussion of additional nonlethal anthropogenic threats during migration beyond those we review here.

**Anthropogenic Structures**

Since the industrial revolution, human-made elements in the airspace have become an increasingly common barrier to migratory movements. Bird mortality from collisions with aircraft, overhead cables, cars, and modern wind turbines have been recorded for a century or more (Coues 1876, Spiker 1927, White 1927, Stoner 1936, Rogers et al. 1977, Sodhi 2002,

McKee et al. 2016), but recent human development has greatly increased hazards to birds in flight (Lambertucci et al. 2015). Birds collide with anthropogenic structures throughout the Nearctic-Neotropical migration system (Agudelo-Álvarez et al. 2010, Calvert et al. 2013a, Menacho Odio 2015, Loss et al. 2015b, Santiago-Alarcon and Delgado-V 2017, Hager et al. 2017, Santos et al. 2017, Gómez-Martínez et al. 2019, Escobar-Ibáñez et al. 2020, Pinto et al. 2020), with collisions resulting in the deaths of more than 1 billion birds per year in Canada and the U.S. alone (reviewed by Calvert et al. 2013b, Loss et al. 2015a). Similarly, collisions have been documented throughout the Afro-Palearctic migration system (Marques et al. 2014, Bernardino et al. 2018, Perold et al. 2020, Mansouri et al. 2022) and the Central Asian flyway (Uddin et al. 2021). Not all collisions result in observed mortality: only a small percentage (approximately 6-7%) of collisions at residential buildings are immediately fatal (Kummer and Bayne 2015, Samuels et al. 2022). Estimating the number of collision-related mortalities is therefore challenging because injured birds may move away from the point of impact before dying, where their carcasses are less likely to be detected and the cause of death identified (Drewitt and Langston 2008, Samuels et al. 2022). Many window strike survivors depart immediately or shortly after impact, but the longer-term survival probability for both groups remains largely unknown (Klem 1990).

In addition to delayed mortality, collisions with structures can have nonlethal effects that impose a fitness cost. The most frequent injury in birds surviving collisions is intracranial hemorrhaging (Klem 1990, Fornazari et al. 2021). Research on traumatic brain injuries (TBIs) in humans and model animals provides insight into the potential consequences for birds. TBIs result in cognitive impairment (slowed reaction times), amnesia, balance impairment, and sleep/wake disturbance (McCrory et al. 2017). Symptoms can persist for days in animals (Giza and Hovda

2001), which could impair a bird's ability to refuel and migrate. Collisions may also reduce flight performance and affect a bird's ability to continue migrating (Orłowski and Siembieda 2005, Travers et al. 2021) or to properly orient itself. A radio-tagged Gray Catbird (*Dumetella carolinensis*) that survived a collision in the midwestern U.S. migrated when it should have been breeding, traveling east in mid-June and south in late June (L. DeGroote, unpublished data), suggesting that the collision affected the bird's ability to orient, navigate, and/or keep track of time. Nonlethal ocular trauma, another common collision-related injury, can become infected or lead to necrosis (Hudecki and Finegan 2018, Demir and Ozsemir 2021). Birds must constantly scan their surroundings to detect predators and find food, meaning that collision-related eye injuries can leave birds vulnerable to predation and less efficient at foraging (Fernández-Juricic 2012).If they manage to reach the breeding grounds, collision survivors with broken or dislocated bones may have lower reproductive success compared to uninjured birds (Townsend et al. 2011). Nonlethal collision injuries can hence affect a bird's ability to evade other threats, reach its intended destination, and/or successfully reproduce.

**Artificial Light at Night**

Artificial light at night (ALAN) is an evolutionarily novel threat that alters the nocturnal landscape with myriad ecological consequences (Rich and Longcore 2006, Burt et al. 2023). Nocturnally migrating birds are attracted to light, whether it is emitted by an artificial (e.g. a floodlight) or natural (e.g., fire) source (Gauthreaux and Belser 2006). ALAN can cause direct mortality: nocturnal migrants attracted to bright floodlights pointing upwards are unable to escape their influence (i.e., the entrapment effect) and fall to their death by exhaustion (Van Doren et al. 2017). Similarly, flares and artificial lights from both onshore (Ramirez Jr. et al. 2015) and offshore oil and gas drilling platforms can attract and disorient birds that die of

exhaustion, inhalation of toxic compounds, or incineration (reviewed in Ronconi et al. 2015). Light pollution increases migrating birds' risk of collisions with human-made structures (Winger et al. 2019a, Van Doren et al. 2021), increasing the risk of immediate mortality (Buchan et al. 2022).

Birds that manage to escape entrapment or burning may still suffer exhaustion or injury, reducing flight performance and possibly limiting a migrant's ability to reach a suitable stopover site for recovery. At the very least, the deviation from their typical route is likely a waste of precious energy (Day et al. 2015). Light pollution typically attracts migrating birds (Gauthreaux 1982, Gauthreaux and Belser 2006, Evans et al. 2007, Poot et al. 2008, Zhao et al. 2014, Rebke et al. 2019), but there is some evidence of avoidance of ALAN (McLaren et al. 2018, Cabrera-Cruz et al. 2020). Attraction to and avoidance of lights may increase the tortuosity of birds' flight paths at the local scale (e.g., Cabrera-Cruz et al. 2021), or the circuitousness of their migration routes at broad spatial scales (Korpach et al. 2022), and energy expenditure in flight increases with path sinuosity (Amélineau et al. 2014). By traversing a nocturnal landscape scattered with ALAN, birds are periodically prone to being attracted to or repelled by lights along their entire migration route, with increased energy requirements accumulating throughout the migration season (Cabrera-Cruz et al. 2018b). Birds may require longer stopovers to compensate for the increased travel distance, and/or may have lower body condition upon reaching their post-migration destination.

ALAN can also directly influence a migrant's energetic condition. Fat deposition of migrating birds is regulated by photoperiod and hormones (Odum 1960, Cornelius et al. 2013, Eikenaar and Schläfke 2013, Robart et al. 2018). For example, melatonin production, the mechanism linking photoperiod to behavior, is reduced by ALAN (Dominoni et al. 2013a). Both

the perception of photoperiod and the production of hormones are disrupted by artificial lights (Liu et al. 2022) with potential cascading effects. The disrupted photoperiod of migrating birds stopping over in heavily light-polluted areas may affect their ability to rest and refuel, potentially leading to delayed departure and late arrival to their post-migration destination. However, recent evidence from captive studies showed that exposure to ALAN did not affect metabolic rate nor food consumption in two migratory sparrows (Litt-Jukes 2023). Fat deposition rates of migrating birds stopping over in some, presumably light-polluted, urban parks are reportedly similar as those in more natural and presumably darker areas (Seewagen and Guglielmo 2010, 2011), though it is unclear whether this result can be generalized to all urban green areas. On the other hand, artificial lights increase the production of testosterone in birds (Dominoni et al. 2013b, Ouyang et al. 2018), increased testosterone advances migratory departure in spring (Tonra et al. 2011, Owen et al. 2014), and ALAN-exposed birds depart and arrive earlier to their destination (e.g., Smith et al. 2021). While testosterone levels were not measured by Smith et al. (2021) and hence a link between this hormone, ALAN, and departure dates has not been established, this question warrants further investigation. Advancing departure could hypothetically increase competitive ability at the destination but might also increase dangerous phenological mismatches.

**Noise Pollution**

Human development is accompanied by noise from sources such as transportation, construction, energy extraction and generation, and military activities (Shannon et al. 2016, Slabbekoorn et al. 2018). Human activity can generate low-frequency noise that propagates over long distances (Ortega 2012), and the extent and ubiquity of road and air travel networks means that even protected natural areas are not safe from noise pollution (Arévalo and Newhard 2011, Barber et

al. 2011, Buxton et al. 2017). In North America, road networks extend millions of kilometers and stopover sites are commonly surrounded by roads (Buler and Dawson 2014, Amaya-Espinel and Hostetler 2019).

Noise pollution is one of the few anthropogenic threats that rarely causes avian mortality. Instead, anthropogenic noise typically affects birds nonlethally by interfering with inter- and intraspecies communication, inducing stress, or causing birds to alter their behavior and habitat use (Patricelli and Blickley 2006, Herrera-Montes and Aide 2011, Ortega 2012, Shannon et al. 2016). In general, birds perceive sudden and unpredictable sounds as threatening and respond as if faced with a predator, whereas chronic noise impedes detection of cues from conspecifics, heterospecifics, or the environment (deemed the "detection-interference continuum" by Francis and Barber 2013). Many birds avoid noisy habitats altogether; those that remain may adjust their vocal behavior to compensate for chronically noisy environments, including vocalizing at higher frequencies, volumes, or at different times (Ortega 2012, Francis and Barber 2013, Slabbekoorn et al. 2018).

Anthropogenic noise can negatively affect stopover habitat use by migrating birds. Broadcasting highway traffic noise from speakers at an autumn stopover site caused a reduction in bird abundance, and several species avoided this "phantom road" entirely (McClure et al. 2013). Noise can mask acoustic cues that birds use to detect predators or prey, hindering their ability to escape or find food (Francis and Barber 2013). In noisy environments birds may increase their vigilance to reduce predation risk, leaving less time for foraging (Francis 2015, Ware et al. 2015, McClure et al. 2017). Consequently, migrating birds remaining at noisy stopover sites may suffer reduced body condition and ability to improve body condition over time (Francis 2015, Ware et al. 2015).

Migrating birds may use anthropogenic noise to decide where and when to stop over: (Cabrera-Cruz et al. 2019) found that birds increase flight altitude when migrating over urban areas and hypothesized that noise pollution can deter them from landing. Anthropogenic noise may also interfere with information that migrants use to assess habitat during both flight and stopover periods. Migrants can use social information from other birds, including acoustic cues, when deciding where to stop over (Chernetsov 2006, Németh and Moore 2014), and sound may be especially important at night when visual cues are largely absent (Mukhin et al. 2008). Migrants also use social learning from conspecifics and heterospecifics to assess the location of quality food resources, competitors, and predators at unfamiliar stopover sites (Németh and Moore 2014, Deakin et al. 2021, de Zwaan et al. 2022, Aikens et al. 2022). Consequently, noise pollution that masks important acoustic cues from avian communities, prey, or predators may reduce birds' ability to quickly and safely refuel, affecting their condition and migration timing and ultimately their fitness.

**Environmental Contaminants**

Humans' production and use of toxic substances has increased dramatically over the past century (Bernanke and Köhler 2009). Migrating birds may be particularly vulnerable to toxicant ingestion since they must rapidly gain mass at unfamiliar stopover locations to replenish fat and lean mass catabolized during flight (Bairlein and Gwinner 1994, Klaassen et al. 2012, Seewagen et al. 2016, Seewagen 2020). Environmental toxicants fall into a wide variety of classes; here we focus on two widespread and well-studied categories – insecticides and heavy metals – as examples of how toxicants can have sublethal effects on migrating birds**.** While migrating birds may be exposed to a range of other contaminants, including polychlorinated biphenyls, polycyclic aromatic hydrocarbons, and oil spills (Tanabe et al. 1998, Henkel et al. 2012,

Bianchini and Morrissey 2018), a complete review of contaminant threats is outside the scope of this paper and has been undertaken elsewhere (e.g., Richard et al. 2021, Ma et al. 2022).

Insecticides have a substantial environmental impact and are estimated to kill millions of birds globally every year (Gaston et al. 2003, Pimentel 2005). Insecticides include compounds in the classes of organochlorines, organophosphates, carbamates, and neonicotinoids (Richard et al. 2021). Organochlorines (OCs) are the oldest class and infamously include DDT, the use of which has been heavily restricted in North America since the 1970s, though its residues and metabolites are still detectable (Jaga and Dharmani 2003). Organophosphates (OPs) and carbamates were introduced after OCs (Cid et al. 2007, Stehle et al. 2018). Neonicotinoids are the newest class and currently the most widely used insecticide in the world (Goulson 2013). They are highly water soluble (Jeschke et al. 2011) and can accumulate in soil (Huang et al. 2020) and aquatic systems (Hladik et al. 2018) where they can harm aquatic invertebrates (Morrissey et al. 2015).

All of the insecticide classes described here have the dose-dependent potential to be immediately lethal to birds, but sublethal effects can also occur depending on the concentration to which a bird has been exposed, length of exposure, and other factors (Bernard 1966, Seabloom et al. 1973, Reece and Handson 1982, Augspurger et al. 1996, Mason et al. 2013, Lopez-Antia et al. 2013, Mitra et al. 2018). Insecticide overuse is contributing to steep insect population declines (Sánchez-Bayo and Wyckhuys 2019, van der Sluijs 2020, Barmentlo et al. 2021), reducing prey availability for insectivorous birds including at stopover sites, and likely contributing to insectivore population declines (Benton et al. 2002, Nebel et al. 2010, Bowler et al. 2019, Møller 2019, Spiller and Dettmers 2019).

Insecticide residues and metabolites can bioaccumulate in birds (Mora et al. 1987, Harris et al. 2000, Kesic et al. 2021) and may be mobilized from the catabolism of tissues during

physically rigorous activities like migration (Tanaka et al. 1986, Colabuono et al. 2012). They may impact neurological development and function (Iwaniuk et al. 2006) or cause appetite suppression and anorexia (Friend and Trainer 1974, Grue 1982, Elliott and Bishop 2011, Lopez-Antia et al. 2013), potentially delaying migration through reduced refueling. Neonicotinoids can also negatively affect blood chemistry (Lopez-Antia et al. 2015) and immune health (Kammon 2012). Sublethal doses of a neonicotinoid caused significant decrease in food consumption, body mass loss (possibly due to appetite suppression), and delayed departure timing in White-crowned Sparrows (*Zonotrichia leucophyrs*) during migration (Eng et al. 2019). Ingestion of some OPs and neonicotinoids can also impair migratory orientation (Vyas et al. 1995, Eng et al. 2017).

Lead and mercury are two of the most common and harmful metal contaminants in the environment, though many others exist (see for example Larison et al. 2000, Burger et al. 2015). Lead exposure is estimated to directly kill 1 million birds per year across Europe and killed 1.6 - 2.4 million birds annually in the U.S. before the widespread adoption of nontoxic gunshot (Pattee and Pain 2002, Pain et al. 2019). We found no annual estimates of mortality from mercury, but evidence suggests that mercury exposure may decrease the probability of survival during migration (Ma et al. 2018). Birds bioaccumulate both metals (Rimmer et al. 2005, Roux and Marra 2007, Edmonds et al. 2012, Burger et al. 2015, Langner et al. 2015), with lead toxicity observed in migrating vultures (Kenny et al. 2015) and waterfowl during spring migratory staging (Havera et al. 1992). Lead toxicity has also been observed in songbirds near contaminated areas (Beyer et al. 2013). Similar to certain pesticides, the physical exertion of migrating can mobilize methylmercury, the most bioavailable and harmful form of mercury, stored in tissues (Seewagen et al. 2016). Exposure to lead and methylmercury can hinder migration by interfering with refueling and reducing flight endurance and performance through a

wide variety of effects that include altered immune function, anorexia, lethargy, ataxia, progressive weakness, diarrhea, convulsions, and paralysis (Vallverdú-Coll et al. 2015, Ma et al. 2018, Williams et al. 2018, Pain et al. 2019, Seewagen et al. 2022). Widespread environmental contaminants thus negatively affect fitness by degrading the health, energetic condition, and orientation ability of migrating birds.

**Free-roaming Domestic Cats**

Introduced mammalian predators pose a major threat to bird species worldwide, driving biodiversity declines and extinctions across a wide range of taxa (Courchamp et al. 2003, Doherty et al. 2016a, Lees et al. 2022). At broad scales, migrating birds frequently stop over in coastal regions, which are also areas of rapidly increasing human development (Buler and Moore 2011, Cohen et al. 2017). While even small parks within the urban or agricultural matrix can provide essential stopover habitat (Seewagen and Slayton 2008, Seewagen and Guglielmo 2010, 2011; Amaya-Espinel and Hostetler 2019, Cohen et al. 2022b, Guo et al. 2023), they may simultaneously host high numbers of novel predators (With 2002). In this section, we focus on free-roaming domestic cats because of their global distribution, abundance, and documented impacts on birds throughout the annual cycle (Loss et al. 2022). While other introduced mammalian (e.g., Courchamp et al. 2003, Doherty et al. 2016) and reptilian (e.g., Kraus 2015) predators also threaten birds, their impacts largely result from predation during the breeding season. We did not find sufficient evidence of other introduced predators' nonlethal effects on migrating birds to include them in this review, but acknowledge such effects may exist.

The lethal effects of free-roaming domestic cats on birds are well-documented; cats are estimated to kill billions of birds annually (Blancher 2013a, Calvert et al. 2013b, Loss et al. 2013a, Li et al. 2021, Stobo-Wilson et al. 2022) and have been implicated in the extinctions of at

least 40 bird species worldwide (Doherty et al. 2016a). While there are few estimates of how many birds are killed during migration versus other periods of the annual cycle, 22% of observed mortalities at a stopover site in South Korea were attributed to cat predation (Bing et al. 2012). The abundance of both unowned and owned free-roaming cats increases with human population density _, and birds migrating through increasingly urbanized regions may be more likely to encounter cats than in other parts of their ranges.

Nonlethal fitness costs of domestic cats likely arise from birds' antipredator responses (Cresswell 2008a), which can include increased vigilance, flocking, foraging in closer proximity to cover, or avoiding risky habitats altogether (Lindström 1989a, 1990; Lind and Cresswell 2006a). Behaviors such as vigilance and habitat switching can reduce risk, but migrating birds that reduce their foraging intensity or avoid locations with the best food resources may suffer lower fuel deposition rates or depart from stopover sites with less fuel (Alerstam and Lindström 1990).

While we know of no published studies investigating migrants' behavioral responses to free-roaming cats during stopover (*but see Nemes et al. in prep*), studies of their responses to native predators can provide insights American Redstarts (*Setophaga ruticilla*) and Blue-gray Gnatcatchers (*Polioptila caerulea*) on stopover foraged in denser cover when migrating hawks were more abundant; gnatcatchers also responded to artificial raptors by moving deeper into shrubs and reducing their activity levels (Cimprich et al. 2005a). During fall migration in the U.S., birds were more abundant in habitat patches where there was no tradeoff between food resources and safety from hawk predation (McCabe and Olsen 2015). Flocks of Bramblings (*Fringilla montifringilla*) on stopover in Sweden maximized their energy intake but experienced more raptor attacks when feeding in agricultural fields; in years when beech mast was abundant

they switched to feeding in forests to reduce predation risk, despite refueling more slowly in this habitat (Lindström 1990).

Migrating birds can also reduce their predation risk by carrying lower fuel loads, as increased fat stores reduce take-off ability and flight maneuverability (Kullberg et al. 1996, 2000). However, departing from stopover with less fuel means flying a shorter distance before stopping, which may slow the migration rate and impose delayed costs in the form of lower reproductive potential (Lindström 1990). Lean birds tend to take more risks than fat ones (Cimprich and Moore 2006); one study found that birds killed by cats on stopover weighed less than live birds caught at a nearby banding station and surmised that the leaner birds took more risks while foraging, increasing their susceptibility to cat predation (Dierschke 2003a).

Based on migrating birds' responses to native predators, we also expect them to respond to free-roaming cats in ways that reduce their risk of death (though see Hamer et al. 2021 for a discussion of differences in prey responses to native versus introduced predators). While antipredator behaviors benefit individual migrants by increasing their short-term survival, they may come at the expense of migration speed or efficiency (Alerstam and Lindström 1990, Lind and Cresswell 2006a). At the population level, the fitness costs of such "non-consumptive effects" can even outweigh the "consumptive effects" of predation (Preisser et al. 2005, Hamer et al. 2021). Consequently, despite the current lack of research on how free-roaming cats influence birds on stopover, we surmise that the ubiquity and abundance of this introduced predator across the migration landscape (Doherty et al. 2016a, Aegerter et al. 2017, Loss et al. 2022) could translate into substantial nonlethal fitness costs by affecting energetic condition and timing (Cresswell 2008a, Loss and Marra 2017a).

**Introduced Plants**

With more than 13,000 species of vascular plants naturalized beyond their native habitat (van Kleunen et al. 2015), and with new introductions occurring unabated (Seebens et al. 2017), it is almost inevitable that migrating birds will stop over in habitats with introduced plants during their journeys. While not all introduced species are harmful, we use the term "introduced" as a more inclusive alternative to "invasive" when referring to species that have negative ecological consequences (Cheng et al. 2023). Migrants can suffer direct mortality from introduced plants in the form of entanglement (Underwood and Underwood 2013, Arcilla et al. 2015) or overconsumption of toxic berries (Lincoln 1931); however, introduced plants are more likely to pose a nonlethal threat to migrants.

Introduced plants alter community structure and composition by replacing native species (McKinney 2004, Burghardt et al. 2009, Nelson et al. 2017), thereby reducing stopover habitat quality (McWilliams et al. 2004, 2021; Guglielmo et al. 2017). Native fruits often contain greater concentrations of energy, fat, or antioxidants than introduced ones(Bolser et al. 2013, Smith et al. 2013, Oguchi et al. 2017). Important nutritional components of berries including carotenoids serve as antioxidants and immune stimulants in birds (Costantini and Møller 2008). As a result, fall migrants are more likely to settle into habitats with fewer introduced plants and preferentially consume native fruits before introduced ones when available (Bolser et al. 2013, Oguchi et al. 2017, 2018; Gallinat et al. 2020). Migrants that use stopover habitats with more introduced fruiting plants have lower concentrations of triglycerides in their bloodstream, indicating poorer refueling performance (Smith and McWilliams 2010, Smith et al. 2015). However, energy or antioxidant content differs among introduced plants and can be comparable between native and introduced species for some genera (ex. *Viburnum;* (Cullen et al. 2020). Despite the evidence

that native fruits are nutritionally superior and preferred by migrants over introduced fruits, their effects on stopover duration and subsequent migratory performance have not yet been fully investigated.

Introduced plants can influence prey availability and migrant behavior at stopover sites (Burghardt et al. 2010, Narango et al. 2017, van Riper et al. 2018). In the southwestern U.S., riparian areas with both native cottonwood-willow habitat and introduced saltcedar (*Tamarix* spp.) have greater diversity and abundance of migrants during spring migration than either habitat independently (Walker 2008, Fischer et al. 2015). Native cottonwood-willow habitat possessed more arthropod biomass during spring migration than introduced saltcedar habitat (Cerasale and Guglielmo 2010). Although saltcedar-dominated riparian areas are avoided by most spring migrants (Fischer et al. 2015), Wilson's Warblers (*Cardellina pusilla)* released from interspecific competition experienced greater refueling performance in this habitat (Cerasale and Guglielmo 2010). Conversely, in northern Iberia, Sedge Warblers (*Acrocephalus schoenobaenus*) experienced lower fuel deposition rates and departed introduced saltbush (*Baccharis halimifolia*) habitats more quickly than native reedbeds (*Phragmites* spp.; (Arizaga et al. 2013). Although complex interactions between or within trophic levels can sometimes result in migrants exploiting novel stopover habitats to their benefit (e.g., Besterman et al. 2020) introduced plants can also negatively influence migrant condition and possibly timing, which could reduce reproductive success or future survival.

**Wildfires**

Humans have increased the frequency, severity, and spatial extent of wildfires by igniting fires (Pechony and Shindell 2010), through fire suppression and land use practices (Bowman et al.

2011), and by inducing climate change, which has intensified storms and altered temperature and precipitation patterns (Krawchuk et al. 2009, Jolly et al. 2015, Martinuzzi et al. 2016). For example, because of increasing spring temperatures, lower winter precipitation, and earlier snowmelt, "wildfire season" in western North America starts earlier and lasts longer than in the past and now coincides with part or all of spring and fall migration for many birds (Westerling et al. 2003, Westerling 2016, Overton et al. 2022). Thus, we classify extreme wildfires as an "anthropogenic threat" while acknowledging the natural origin of many fires (Bowman et al. 2011), the dependence of many ecosystems on healthy fire regimes (McLauchlan et al. 2020), and the importance of Indigenous fire stewardship to biodiversity conservation (Hoffman et al. 2021).

Annual mortality estimates are scant, but severe wildfires were estimated to kill over one million birds in Brazil in 2020 (Tomas et al. 2021). Wildfires can kill birds directly via burning or smoke inhalation (Whelan et al. 2002, Engstrom 2010, Sanderfoot and Holloway 2017, Nimmo et al. 2021, Sanderfoot et al. 2021, Jolly et al. 2022). Migrating birds may be burned if they inadvertently fly too close to fires; studies have documented this phenomenon with wildfires, but a lumberyard fire in the U.S. killed several dozen nocturnal migrants that flew too low over the flames (Stone 1906), and gas flares at offshore oil and gas drilling platforms regularly kill migrating birds through burning or inhalation of toxic emissions (Bjorge 1987, Ronconi et al. 2015). Nocturnal migrants disoriented by firelight and smoke might also fatally collide with one another in midair, as has occurred with other light sources (Gauthreaux and Belser 2006).

The efficiency of avian respiratory systems may increase their susceptibility to toxic compounds in wildfire smoke, including carbon monoxide, particulate matter, and hydrogen

cyanide (Sanderfoot and Holloway 2017, Sanderfoot et al. 2021). In the summer and autumn of 2020, citizen scientists documented a mass avian mortality event coinciding with a period of severe wildfire activity across the western U.S. that killed an estimated 100,000 - 1 million migrating birds (Kittelberger et al. 2022). Deaths of migrating passerines were correlated with proximity to wildfires and to poor air quality (Yang et al. 2021). Birds captured during this period showed lower body condition and evidence of emaciation (Kittelberger et al. 2022), indicating that fires may have induced birds to depart on migration before they were ready or interfered with their ability to refuel *en route* (Yang et al. 2021, Kittelberger et al. 2022).

Researchers have recently documented in-flight behavioral responses to wildfires in bird species large enough to carry GPS trackers. During a period of intense fire activity in western North America, migrating Tule Greater White-fronted Geese (*Anser albifrons elgasi)* responded to high smoke concentrations by landing prematurely, changing the direction of their flight paths, or attempting to fly over smoke plumes (Overton et al. 2022). Several geese that encountered smoke during overwater flights landed on the water; some made inland stopovers that were far from their typical migration routes. Birds' efforts to circumnavigate smoke plumes increased the distances they traveled and doubled the time they spent on migration (Overton et al. 2022). The energetic cost of avoiding wildfires while migrating is probably substantial (Kittelberger et al. 2022); the authors estimated that geese would need to forage for an additional 4 - 6 days to compensate for the increased energy expenditure (Overton et al. 2022). While geese avoided wildfires, migrating passerines are frequently attracted to and disoriented by artificial light (see ALAN section above), and might similarly be drawn towards wildfires (Bjorge 1987, Gauthreaux and Belser 2006). Either attraction to or repulsion from the light of wildfires could

cause excess energy expenditure and changes to the migration route, requiring more time to refuel and increasing the total time spent on migration.

**Climate Change**

Human combustion of fossil fuels, along with land-use practices and other activities, induces changes to the global climate that impact biodiversity and biological processes across scales (Parmesan and Yohe 2003, Parmesan 2006, Rosenzweig et al. 2008, Arias et al. 2021). Climate change-related phenological shifts, species range shifts, and altered weather patterns throughout the annual cycle can dramatically alter ecological interactions and increase the challenges of migration (Robinson et al. 2009, Blois et al. 2013, Pearce-Higgins and Green 2014, Kharouba et al. 2018, Bateman et al. 2020), ultimately driving population declines (Northrup et al. 2019). While migrating birds have always had to contend with periods of adverse weather (Newton 2007), climate change may increase mortality during migration by increasing the frequency and severity of extreme weather events (Dale et al. 2001, Martinuzzi et al. 2016, Arias et al. 2021) as well as wildfires. Although migrants typically avoid departing during inclement weather, mass mortality can occur when birds encounter heavy rain, snow, fog or mist, or high winds while in flight (reviewed in Newton 2007).

Nonlethal impacts of climate change on bird migration have been well studied. An exhaustive description is beyond the scope of this review, but we highlight several of the major implications for migrating birds. Climate change can alter the timing of bird migration, particularly in the pre-breeding (spring) season (Saino et al. 2011). Experts disagree on the mechanisms by which phenological changes occur, but there is general agreement on broad patterns (reviewed in Knudsen et al. 2011). Globally, birds are arriving increasingly earlier to their breeding areas (Gordo 2007, Usui et al. 2017), with average advances of 2-3 days per

decade (Romano et al. 2022). Less clear is the mechanism behind this advancement, with earlier departure from non-breeding areas, faster migration speeds, decreased migration distance, or selective pressure for the evolution of earlier phenotypes all supported to some degree (Robinson et al. 2009, Knudsen et al. 2011). Impacts on post-breeding migration timing are less consistent, with no clear global trends in departure timing (Romano et al. 2022) but an overall increase in the duration of fall migration (Zimova et al. 2021, Horton et al. 2023).

Birds might suffer from reduced food availability if their migration timing is out of sync with resource phenology (Carey 2009), a phenomenon called phenological or trophic mismatch. Mismatch between migrants' arrival timing to breeding areas and peak food availability for their offspring has been suggested as a driver of population declines in the Afro-Palearctic migration system (Both et al. 2006, Saino et al. 2011). While phenological mismatches have mostly been studied with regard to arrival timing and resource availability in breeding areas, mismatch with food sources on stopover can reduce refueling ability (Bairlein and Hüppop 2004, Kellermann and van Riper 2015) and potentially migration rate. In some regions climate change has decreased annual rainfall, reducing food availability for migrating birds. For example, low precipitation at an important stopover site impaired the ability of Eurasian Reed-warblers (*Acrocephalus scirpaceus*) to refuel prior to crossing the Sahara Desert, reducing their annual survival (Halupka et al. 2017). Conditions during stopover carry over to affect reproductive phenology as well as success: three species of Afro-Palearctic migrants bred earlier in years when migratory passage areas were warmer, and one species bred earlier in response to higher rainfall on passage (Finch et al. 2014), presumably due to increased insect prey on stopover. Birds that encounter extreme weather *en route* may be forced to make more frequent stopovers,

which reduced subsequent reproductive success in Black-bellied Plovers (*Pluvialis squatarola*) (Clements et al. 2022).

For temperate-breeding birds, warming temperatures may enable some species to spend the stationary non-breeding season closer to their breeding areas, reducing the distances they must travel (Visser et al. 2009, Curley et al. 2020). Other species show the opposite pattern, with proportionally larger northward shifts in breeding latitude resulting in longer average migration routes (Curley et al. 2020). Increases in migration distance due to climate change (Huntley et al. 2006, Robinson et al. 2009, Zurell et al. 2018) may necessitate longer or additional stops for birds to refuel (Schmaljohann and Both 2017, Howard et al. 2018) and could expose them to additional threats *en route* or reduce time available for other life history events, such as reproduction and molt (Carey 2009). Organisms differ in their range shifts and phenological responses to climate change (Parmesan and Yohe 2003, Blois et al. 2013, Kharouba et al. 2018), reshuffling ecological communities and potentially further influencing food sources (Bairlein and Hüppop 2004) or migrants' interactions *en route* (Cohen and Satterfield 2020) disrupting patterns of phenology, weather, and species distributions, climate change alters birds' migration timing, routes, and ability to exploit resources throughout the annual cycle.

**Interacting Threats**

Consensus is emerging that anthropogenic threats act in combination to impact birds and overall biodiversity (Didham et al. 2007, Brook et al. 2008, Dutta 2017, Isbell et al. 2022, Kimmel et al. 2022). Migrating birds are exposed to multiple anthropogenic factors *en route* and often encounter several threats at once (Figure 3). Many of the threats we have discussed abound in urban and industrial areas, effectively transforming these into hubs for the interaction of threats and facilitating their negative effects (Richard et al. 2021). Similarly, agricultural intensification

is a source of multiple threats such as environmental contaminants, habitat loss, noise pollution, and introduced flora and fauna (Stanton et al. 2018), all of which can interact to harm migrating birds. Threats may be additive, where their combined effect is equal to the sum of the independent effects, or synergistic, where the combined effect is greater than the sum of the individual effects (Darling and Côté 2008). For example, noise pollution reduces bird abundance during stopover (McClure et al. 2013) but its influence is greater when ALAN is also present, and some species are affected only when light and noise co-occur (Wilson et al. 2021).

Threats interact in complex ways, and the effect of a single threat may expose birds to one or more other stressors. For instance, attraction to ALAN can increase risk of collisions with structures (Gauthreaux and Belser 2006), particularly during inclement weather (Newton 2007). Furthermore, the combination of ALAN and collisions increases mortality by introduced predators because free-roaming domestic cats and dogs prey on unconscious or stunned birds after window collisions (Rebolo-Ifrán et al. 2021). ALAN can also increase mortality from native predators that hunt nocturnally migrating songbirds that are attracted to or disoriented by city lights (DeCandido and Allen 2006). Birds' antipredator responses to free-roaming cats, such as vocalizing and mobbing behavior, may also draw the attention of native predators. For example, breeding birds that are distracted or agitated by free-roaming cats suffer increased nest predation rates by native corvids (e.g., Bonnington et al. 2013) and raptors (Greenwell et al. 2019). Chronic noise pollution is higher in urban areas (Ortega 2012) and may mask the acoustic cues that migrating birds use to perceive predators or to communicate the threat of predators to other individuals (Francis and Barber 2013, but see Pettinga et al. 2015).

Birds that are weak, ill, or disoriented from exposure to adverse weather (Newton 2007) or wildfire smoke (Sanderfoot et al. 2021) may be more susceptible to predation during stopover.

Both native and introduced predator species in fire-adapted ecosystems, including free-roaming cats, exploit fire to hunt fleeing prey or hunt more effectively in recently burned areas (Doherty et al. 2022). Similarly, birds experiencing neurological impairment, mass loss, or immunosuppression from ingestion of pesticides or heavy metals could be more susceptible to building strikes, extreme weather stress, vagrancy, or predation during migration (Galindo et al. 1985, Eng et al. 2017, 2019; Seewagen 2020), though these interactions are not often studied explicitly. Captive studies have demonstrated that birds dosed with pesticides are more susceptible to domestic cat predation (Galindo et al. 1985).

Attraction to artificial lights may increase migrants' exposure to air pollution and toxicants from urban areas (La Sorte et al. 2022) and oil flares (Bjorge 1987). Birds can experience co-toxicity when exposed to multiple environmental pollutants (Richard et al. 2021), and the immunosuppressive effects of certain contaminants together with natural reductions in immune response during migration might render migrating birds especially vulnerable to disease (Gylfe et al. 2000, Owen and Moore 2006, Chatham-Stephens et al. 2013, Vallverdú-Coll et al. 2015).

Anthropogenic climate change alters weather patterns, phenology, and species distributions in ways that can increase birds' exposure or susceptibility to other threats (Fig. 3B). Harmful introduced species show range expansions with climate change (Parmesan and Yohe 2003, Hellmann et al. 2008), which may increase migrants' probability of encountering these threats *en route* (Robinson et al. 2009, Bateman et al. 2020, Kubelka et al. 2022). Climate change also disrupts both the timing of bird migration and the fruiting phenology of introduced plants, which could affect availability of preferred foods during stopover (Gallinat et al. 2020). While

researchers and conservation managers often consider threats to wildlife in isolation, interactions among threats should not be overlooked when evaluating the fitness costs to migrating birds.

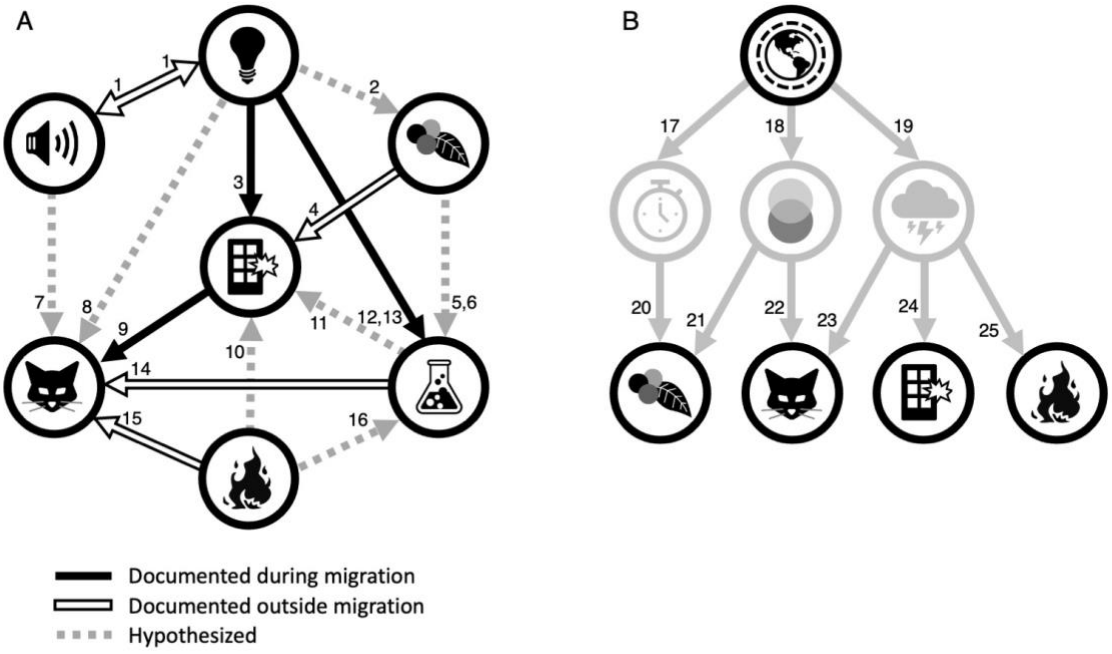


**Figure 3.** Anthropogenic threat sources can interact to produce cumulative or synergistic effects on migrating birds. (A) We found a small number of published studies documenting interactions between pairs of threats during migration (black arrows), as well as studies that documented threat interactions affecting birds outside of the migration period (or affecting non-migratory species) that we imagine could also occur during migration (white arrows). We hypothesize that additional interactions between threats are possible but did not find published evidence for them (gray dashed arrows). Numbers at the head of each arrow denote the corresponding source(s); for hypothesized interactions, sources provide evidence for how expected interactions might arise. Threat symbols are as follows (clockwise from top in 3A): artificial light at night (light bulb icon), introduced plants (berry and leaf icon), environmental contaminants (flask icon), wildfires (fire icon), free-roaming domestic cats (cat icon), noise pollution (speaker icon), and collisions (center; window icon). (B) By altering migration phenology (clock icon), inducing range shifts (shaded circles icon), and increasing the frequency of extreme weather events (lightning storm icon), climate change (earth icon) may increase migrating birds' exposure to introduced plants, introduced predators, collisions, and wildfires. For clarity, we only provide example citations in the figure rather than an exhaustive list of all sources relevant to a given interaction. Figure citations: [1]Wilson et al. 2021, [2]Dolan et al. 2011, [3]Gauthreaux and Belser 2006, [4]Kinde et al. 2012, [5]Quinn et al. 2006, [6]DeCandido & Allen 2006, [7]Rebolo-Ifrán et al. 2021, [8]Newton 2007, [9]Mineau & Tucker 2002, [10]La Sorte et al 2022, [11]Russell 2005, [12]Shimeta et al. 2016, [13]Bautista 2007, [14]Galindo et al. 1985, [15]Doherty et al. 2022, [16]Vyas et al. 2009, [17]Robinson et al. 2009,

[18]Bateman et al. 2016, [19]Martinuzzi et al. 2016, [20]Gallinat et al. 2020, [21]Blois et al. 2013, [22]Hellmann et al 2008, [23]Hilton et al. 1999, [24]Loss et al. 2020, [25]Bateman et al. 2020.

**Knowledge Gaps and Future Directions**

This review highlights a number of important shortcomings in our understanding of anthropogenic threats to migrating birds. Arguably, the most critical unanswered question is the extent to which nonlethal effects during migration contribute to population declines. We have outlined potential ways that exposure to nonlethal anthropogenic hazards, singly or in combination, can impose fitness costs. In practice, nonlethal effects that occur during migration are extremely difficult to link to population trends; the same is true for even well-documented mortality sources (Loss et al. 2012, Rosenberg et al. 2019, thought see Hewson et al. 2016). This knowledge gap is due to several critical limitations inherent to studying migratory animals. First, movements are difficult to track: populations differ in their migration routes and timing, and individuals of many species are too small to track their migrations in real time. Second, as birds migrate, experiences at one site may carry over to reduce fitness at a later time and place, making it difficult to pinpoint the consequences of nonlethal stressors and their interactions. Finally, there is a geographic bias in migration studies (Wilson et al. 2016, Fernández-Arellano et al. 2021, Soares et al. 2023) that makes it difficult to quantify the effects of threats with variable occurrence throughout the migratory route. Below, we describe these limitations in further detail while suggesting experimental and theoretical approaches to address these knowledge gaps.

One difficulty in linking *en route* anthropogenic threats to population declines is that populations may vary in their migratory timing and routes, exposing them to different levels of risk (Kirby et al. 2008, Hewson et al. 2016, Pearce-Higgins et al. 2017). We have a poor understanding of migratory connectivity for most species (Cohen et al. 2018, Marra et al. 2019),

further hampered by the fact that many individuals are too small to track their migrations in real time. A variety of approaches, separately or in combination, can help fill these knowledge gaps (Katzner et al. 2020, Marcacci et al. 2022). To identify where and when bird populations are exposed to threats during migration, a better understanding of migratory connectivity (Webster et al. 2002, Cohen et al. 2019) together with spatially explicit threat maps across entire migration corridors (Tulloch et al. 2015, Bowler et al. 2020, Buchan et al. 2022) will prove invaluable. Because many threats extend upwards to impact migrants in flight, three-dimensional hazard maps could help protect important airspace corridors (Davy et al. 2017, Cohen et al. 2022a). Incorporating a temporal component to create dynamic threat maps can more accurately capture the seasonal ebbs and flows in risk that birds experience as they move across continents (Runge et al. 2016, Bauer et al. 2019). Mapping spatiotemporal patterns of risk as well as migration bottlenecks (Buehler and Piersma 2008, Bayly et al. 2018, Gómez et al. 2019, Horton et al. 2019a) and important stopover sites (Buler and Dawson 2014, Xu et al. 2020, Cohen et al. 2021, Guo et al. 2023) can inform the design of dynamic rather than static protected areas that enable safe passage at the times and places when it is most critical for migratory species (Runge et al. 2014).

Over broad spatial scales, environmental conditions *en route* influence migration timing and survival (Tøttrup et al. 2012, Briedis et al. 2017), but less clear are any compounding effects of more localized threats or of repeated exposure throughout the migration period. We can imagine that a bird that sustains an injury at one stopover site presumably remains at increased risk of predation at subsequent stopover sites, unless and until it has fully recovered, but few studies have examined how long nonlethal effects persist. There is increasing evidence that conditions at a single stopover site can carry over to affect later survival and reproduction (e.g.,

Halupka et al. 2017, Clements et al. 2022, Grandmont et al. 2023). For instance, experimental manipulations reveal that Snow Geese (*Anser caerulescens*) exposed to adverse conditions at a single spring stopover site have lower nesting success and may skip breeding altogether, depending on environmental conditions at the breeding grounds (Legagneux et al. 2012, Grandmont et al. 2023).

A variety of experimental and theoretical methods can help quantify the effects of nonlethal threats and their interactions. Researchers can couple individual migration tracking with experimental manipulations of threat sources (Birnie-Gauvin et al. 2020) or compare the performance of birds tagged at sites with different levels or combinations of threats (Hewson et al. 2016, Sanderfoot et al. 2021) Increased bird banding and tagging efforts in urban and suburban habitats throughout species' non-breeding ranges would provide useful comparisons of the physiology, behavior, and survival of birds exposed to elevated levels of anthropogenic disturbance during migration (Dunn 2016). Although a mechanistic understanding of how nonlethal threats affect migrants often requires isolating threat sources (e.g., McClure et al. 2013) anthropogenic threats rarely occur in isolation in the real world, and single-factor experimental manipulations should be complementary to research on multiple interacting stressors during migration. Theoretical models of behavior, including individual-based models, offer opportunities to investigate how individuals' responses to threats during migration carry over to affect life history events such as reproduction (Bauer and Klaassen 2013). Full annual cycle population models that incorporate the influence of *en route* nonlethal effects on subsequent per capita reproduction and survival or population vital rates (Weber et al. 1999, Norris and Taylor 2006, Ratikainen et al. 2007) can be used to guide future research and inform

spatial and temporal prioritization for reducing nonlethal anthropogenic threats (Sheehy et al. 2011, Hostetler et al. 2015).

Finally, although we did not conduct a systematic review, we noted clear bias in the geographic location of studies on nonlethal effects. For the Nearctic-Neotropical migration system, more research is needed on threats outside of the U.S. and Canada (Bayly et al. 2016, 2018). Likewise, while threats to migrating waterbirds within the East Asian-Australasian migration system have received increasing research attention (Amano et al. 2010, Szabo et al. 2016, Lei et al. 2019, Yong et al. 2021), threats and life history information for other taxa, particularly passerines, are less understood throughout the flyway (Yong et al. 2015, 2018; Yamaura et al. 2017). Similarly, Afro-Palearctic bird migration has been well-studied within Europe and parts of the Middle East, but the basic ecology of birds migrating and wintering in sub-Saharan Africa remains poorly documented (Vickery et al. 2014, Marcacci et al. 2022). These patterns reflect a well-established geographic bias in conservation research and publication (Wilson et al. 2016, MacGregor-Fors et al. 2020, Maas et al. 2021, de Vos and Schwartz 2022, Soares et al. 2023, Ruelas Inzunza et al. 2023) that undermines efforts to protect migrating birds and the ecosystems upon which they rely across the annual cycle. Threats can vary across migration landscapes and between populations of a species based on socioeconomic, geographic, ecological, cultural, and policy differences (Runge et al. 2014, Kark et al. 2015, Horton et al. 2019a, Saunders et al. 2021). For example, while organophosphates have been outlawed in North America since the 1970s, Neotropical migrants may be exposed in parts of their non-breeding ranges where these compounds remain legal (Maldonado et al. 2017). To design effective trans-boundary conservation measures that simultaneously benefit birds and people (Kark et al. 2015), we must understand how the variable occurrence and timing of threats

influence the success of migration through these regions (Runge et al. 2014, 2015; Saunders et al. 2021).

**Conservation Implications**

Why should researchers, conservation managers, and the public be concerned about nonlethal effects of human activity on migrating birds? Alleviating sources of en route mortality will undoubtedly reduce their nonlethal effects as well, but specifically addressing nonlethal effects will also lead to more robust protections. For example, environmental impact assessments that only evaluate direct bird mortality might underestimate the consequences of proposed development in migration corridors, which can degrade terrestrial or aerial habitat for migrating birds without killing them. Conversely, conservation efforts based on an incomplete understanding of if and how nonlethal effects influence fitness may waste limited resources with little benefit for populations (Fraser et al. 2018, Wilson et al. 2020). We surmise that a fuller understanding of how nonlethal effects impact migrants en route will help elucidate why some individuals and populations are more susceptible than others, which will guide targeted conservation measures (Bauer et al. 2019, Katzner et al. 2020).

While comparative estimates of annual mortality from different anthropogenic sources have been derived for several countries (Loss et al. 2012, 2015a; Longcore and Smith 2013, Calvert et al. 2013a), we know of no similar efforts to rank the number of deaths during migration specifically. Our review indicates that most nonlethal effects of anthropogenic threats during migration are even less well documented and quantified than mortality. Furthermore, the magnitude of individual threat effects and their interactions on migrating birds will depend on the local context as well as the species involved, meaning that a single ranking for all taxa and flyways may not be meaningful (Bellard et al. 2022). Consequently, we have not attempted to

rank the importance or severity of nonlethal threats *en route* in this review, but we recognize that with increased knowledge such a ranking would be beneficial for prioritizing conservation action and raising awareness (e.g., Kirby et al. 2008). However, we suggest that threats exhibiting a greater number of interactions with other threats are likely having the largest impact (Figure 3). As an example, ALAN produces documented or hypothesized interactions with five other threats, meaning that alleviating ALAN will concurrently reduce migrating birds' exposure or susceptibility to other anthropogenic hazards. Similarly, at least five threats can increase the vulnerability of migrating birds to free-roaming cats, and thus managing cat populations could reduce the total impact of these threats on migrating birds (Lepczyk et al. 2022).

Another important reason to study and mitigate nonlethal threats is that humans often experience deleterious effects from the same factors that nonlethally affect birds, such as sensory pollution and environmental contaminants (Sandifer et al. 2015, Şekercioğlu et al. 2016, Liang et al. 2020). Thus, alleviating nonlethal effects on migrating birds will simultaneously benefit human health and well-being in ways that measures to reduce direct bird mortality, such as installing bird-safe windows, typically do not (Liang et al. 2020). This provides an opportunity for conservation practitioners to partner with stakeholders who might not otherwise support bird-friendly policies to achieve shared benefits for both migrating birds and public health (Haines-Young and Potschin 2010, Sandifer et al. 2015, Şekercioğlu et al. 2016, Aronson et al. 2017, Decker et al. 2019). In all cases, successfully understanding and reducing both lethal and nonlethal effects of anthropogenic threats across the entirety of bird migration corridors will require international cooperation and input from partners across governments, institutions, and the public (Runge et al. 2017, Bayly et al. 2018, Yong et al. 2018, Marcacci et al. 2022).

## Conclusions

Simply surviving the migratory journey is of little use if birds arrive to their destination too late, unhealthy, or exhausted to successfully reproduce or survive the next season (Hedenström 2008, Senner et al. 2015, Moore 2018). Although challenging to study, understanding how nonlethal effects during migration impose fitness costs that may scale up to influence migratory bird populations, and how effects change or multiply when threats interact, will enhance conservation (Bowlin et al. 2010, Runge et al. 2014, 2015, 2016; Katzner et al. 2020). With migratory species facing steep declines (Rosenberg et al. 2019), the impact of human activity on migrating birds should not be measured solely by mortality, but also in changes to a bird's migration timing, route, and physiological condition (Moore 2018). When we focus exclusively on immediate mortality, we risk underestimating the full costs of human activity on migrating birds and our responsibility to lessen the barriers that impede successful migration.

## Acknowledgments

We are grateful for the invitation to submit this review article by the American Ornithological Society's Lanyon Award Committee. The manuscript has benefitted greatly from the revisions of two anonymous reviewers and the journal editors.

# Chapter 2: Songbirds in North America catch the green wave, but not by surfing

**Chapter Note:** This chapter was submitted for publication and received a decision of revise and resubmit from the *Journal of Animal Ecology* with coauthors Peter P. Marra, Theodore J. Zenzal Jr., Samantha A. Collins, Bryant C. Dossman, Alexander R. Gerson, Camila Gómez, Ana M. González, Mariamar Gutierrez Ramirez, Sarah A. Hamer, Joseph Marty, Phillip L. Vasseur, and Emily B. Cohen.


**Abstract**

1. In temperate regions, the annual pattern of spring onset can be envisioned as a "green wave" of emerging vegetation that moves across continents from low to high latitudes, signifying increasing food availability for consumers.
2. Many herbivorous waterfowl "surf" the green wave, timing their movements to exploit peak vegetation resources in early spring. Though less well studied, secondary consumers such as insectivorous songbirds can track phenological waves during migration as well.
3. We hypothesized that songbirds in eastern North America time their spring migrations to coincide with later phases of vegetation phenology, which correspond to increased arthropod prey, and predicted they would trail behind the green wave rather than surfing its leading edge. We further hypothesized that the rate of the green wave influences bird migration rates, such that individuals adjust migration timing within North America to phenological conditions they experience *en route*.

4. To test our hypotheses, we used the continent-wide Motus automated radio telemetry network to track individual songbirds of four species on spring migration between the southeastern U.S. and northern locations.
5. We measured the green wave using two metrics of spring onset – the normalized difference vegetation index (NDVI) and the spring index first leaf date – then calculated the rate and timing of the green wave relative to bird detections.
6. All individuals arrived in the southeastern U.S. well after local spring onset, behind the leading edge of the green wave. Counter to expectations, we found that songbirds followed a "catching up" strategy: individuals migrated faster than the green wave, effectively closing in on the start of spring as they approached breeding areas.
7. While green wave surfing is a well-documented migration strategy for herbivorous waterfowl and ungulates, songbirds in our study migrated faster than the green wave and increasingly caught up to its leading edge *en route*.
8. Consequently, songbirds experience a range of stages of vegetation development while migrating through North America, suggesting flexibility in their capacity to exploit variable resources in spring.

## Introduction

Migratory behavior has evolved in response to predictable seasonal fluctuations in resources and environmental conditions throughout an animal's annual cycle (Alerstam et al. 2003). In birds, migration timing is governed by evolved circadian and circannual rhythms tied to photoperiod and fine-tuned by environmental conditions, allowing individuals to access resources at the appropriate time both at the destination and *en route* (Gwinner 1996, Carey 2009). However, the exact timing of seasonal transitions such as green-up and green-down varies from year to year, affecting when resources become available to consumers (Melaas et al. 2013, Liu and Zhang 2020). A migratory songbird that arrives to its temperate breeding grounds on the same calendar day each year may find the forest verdant and flush with caterpillars in some springs or bare trees and a dusting of snow in others. While arriving to the breeding grounds earlier than competitors can have reproductive benefits (Kokko 1999, Smith and Moore 2005a), arriving too early can impose physiological or survival costs (Briedis et al. 2017). Consequently, long-distance migrants are expected to adjust the pace of migration in response to the environmental conditions they encounter *en route,* ultimately improving their fitness (Ahola et al. 2004, Tøttrup et al. 2010, Bauer et al. 2020). Plasticity in adjusting migration rate to annual variations in environmental phenology may prove especially important because spring is arriving earlier across the temperate zone due to climate change, with increasing variation in spring onset (Schwartz et al. 2013, Liu and Zhang 2020).

The "green wave hypothesis" offers an explanation for how animals correctly time their migrations, positing that migrants adjust their pace *en route* based on the timing of vegetation growth in the spring (Drent et al. 1978). In many temperate regions, spring onset can be

envisioned as a “green wave” of new plant growth that sweeps across the continent from low to high latitudes and elevations as days lengthen and temperatures rise (Armstrong et al. 2016). This flush of emerging vegetation is followed by a profusion of animal life, including both vertebrate and invertebrate herbivores that directly consume plant growth (Harrington et al. 1999). Migrating organisms that track changing resource phenology and synchronize their movements with vegetation emergence are considered to “surf” the green wave (Drent et al. 1978, van der Graaf et al. 2006). For example, many herbivorous waterfowl and terrestrial ungulates time their migrations to coincide with peak growth of nutritious young foliage in early spring, surfing at the leading edge of the green wave (van der Graaf et al. 2006, Bischof et al. 2012, Aikens et al. 2017). Some herbivores surf behind or ahead of this leading edge depending on the stage (phenophase) of vegetation development they track (Shariatinajafabadi et al. 2014), while others overtake the green wave, effectively jumping over it rather than surfing (Bischof et al. 2012, Kölzsch et al. 2015). The specific strategy (see Fig. 1) may depend on when individuals derive the greatest benefit from high-quality new vegetation growth, either for themselves or their offspring, thereby maximizing fitness (van der Graaf et al. 2006, Armstrong et al. 2016, Abrahms et al. 2021).

Migrants at higher trophic levels may also synchronize their movements to the green wave of emerging vegetation. For example, many songbirds rely on herbivorous prey, primarily caterpillars and other arthropods, to fuel their northward migrations (Wood and Pidgeon 2015). Therefore, the green wave can mean increasing food availability for insectivorous songbird migrants (La Sorte and Graham 2021), with herbivorous caterpillar emergence linked to temperature changes and plant growth (van Asch and Visser 2007, Cayton et al. 2015). In support of the green wave hypothesis for secondary consumers, songbirds can adjust migration

timing in response to spring temperature or vegetation phenology (Tøttrup et al. 2010, Thorup et al. 2017, Youngflesh et al. 2021). However, unlike primary consumers, secondary consumers may be less likely to surf the leading edge of the green wave, instead anchoring their timing to a later phenophase that corresponds to increased arthropod availability (van Asch and Visser 2007, Cayton et al. 2015, Mayor et al. 2017).

In North America, annual variability in the timing of species' migrations between the southern and northern U.S. supports *en route* adjustment to the pace of migration, with faster rates of migration and earlier passage during warmer springs when plants develop earlier (Marra et al. 2005, Hurlbert and Liang 2012). Advancement in spring migration timing within North America measured by weather radar is correlated with increasing spring temperatures linked to climate change (Horton et al. 2020), yet migrants' arrival timing *into* North America in spring has not advanced for birds traversing the Gulf of Mexico (Cohen et al. 2015, Horton et al. 2019b). Taken together, these findings suggest that individual birds fine-tune their migration rate within temperate North America to match phenological conditions *en route* (Marra et al. 2005, Cohen et al. 2015, Horton et al. 2020).

Confirmation that individual plasticity is responsible for observed population-level changes in migration rate and timing requires tracking individuals as they migrate (Charmantier and Gienapp 2014, Thorup et al. 2017, Schmaljohann et al. 2017). This offers advantages over 1) using arrival dates from banding stations, which obscure individual movements and could potentially mask population-specific effects, and 2) continental-scale weather radar observations, which do not differentiate between species or populations. In the last decade, remote tracking of individual songbirds on migration has become possible thanks to technological advances in radio transmitter technology and automated receiving stations (McKinnon and Love 2018). We used

data from four species of migratory songbirds tracked during their spring migrations via the Motus automated radio telemetry network (Taylor et al. 2017) to determine if individuals adjust their migration rate and timing in accordance with the green wave phenology within North America. Migrants were tracked from the northern coast of the Gulf of Mexico to stations further north as they approached their breeding destinations, allowing us to measure migration rate and timing for each individual.

We used several metrics characterizing spring phenology to assess (1) if migrating songbirds adjust migration rate in response to phenological conditions *en route*, and (2) if their migrations are characterized by a particular strategy such as surfing or jumping over the green wave (Fig. 1). We further sought to identify how the strength of species' relationships to the green wave might vary over the course of the season, reflecting changes in the relative importance of exogenous and endogenous drivers of migration phenology (Jenni and Schaub 2003a, Tøttrup et al. 2010).

We expected migrants to adjust migration rate in response to the rate that the green wave travels across the continent in spring. Rather than tracking the wave's leading edge as do many herbivores (Fig. 1., Surfing - Leading Edge), we predicted that insectivorous songbirds would migrate behind the leading edge of the green wave, instead tracking the insects that emerge in response to vegetation green-up (Fig.1, Surfing - Trailing). Alternative strategies are possible when individuals migrate faster between points on the landscape than the green wave; they may begin by trailing behind the green wave but then close in on its leading edge (Fig.1, Catching Up) or even overtake it (Fig. 1, Jumping). We also hypothesized that the cost of phenological mismatch is higher early in the spring and predicted that early individuals would be more sensitive to the green wave rate when adjusting their migration rate. In contrast, we predicted

that later individuals would migrate faster to minimize migration time because of the potential reproductive costs of arriving late to the breeding grounds.

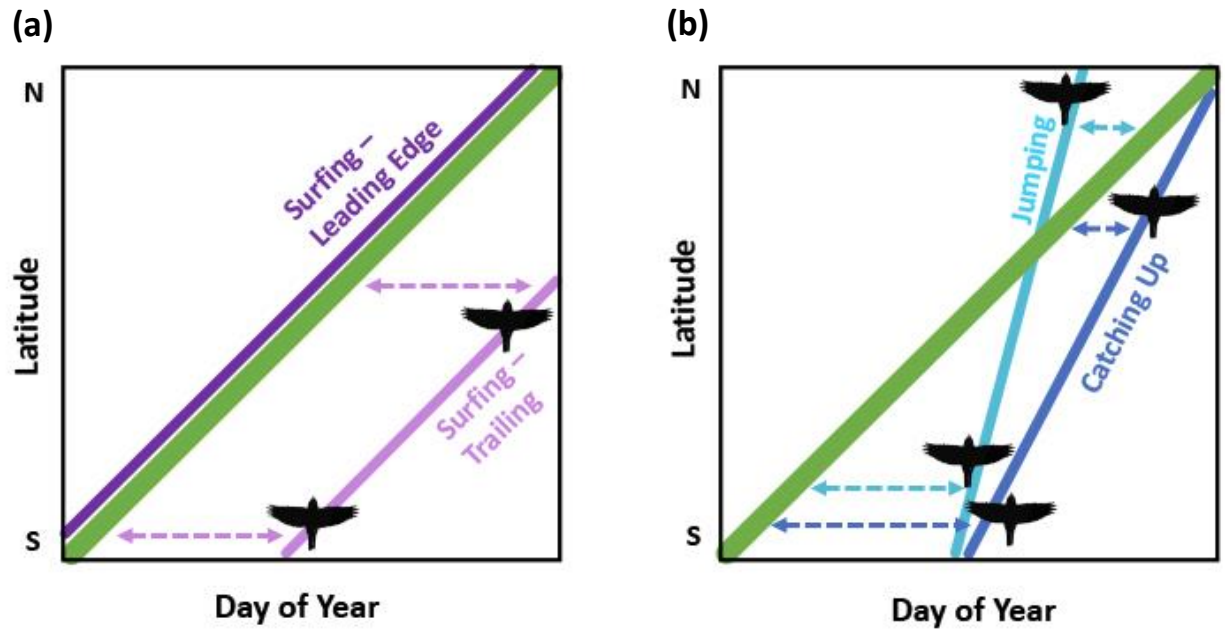


**Figure 1.** Four potential strategies for bird migration relative to the green wave. Birds are assumed to experience different extents of vegetation development depending on their migration timing relative to spring onset day, which signifies the arrival of the green wave (solid green line). The phenological interval (dashed horizontal arrows) is the day of year of the bird's passage minus the day of year of local spring onset. If migration rate matches the green wave rate (a), then the phenological interval will not change as birds move from south to north, although they may migrate with the leading edge of the green wave (Surfing – Leading Edge) or trail behind it (Surfing – Trailing). If birds migrate faster than the green wave (b), the phenological interval will decrease as they travel from south to north, allowing migrants to catch up to the green wave (Catching Up) or overtake it (Jumping).

## Methods

### Migration rate

We tracked four Nearctic-Neotropical songbird species – Swainson's Thrush (*Catharus swainsonii*), Gray-cheeked Thrush (*Catharus minimus*), Northern Waterthrush (*Parkesia novaeboracensis*), and Ovenbird (*Seiurus aurocapilla*) – during spring migration in each of four years (2016 - 2019). Birds were captured and tagged either in stationary non-breeding areas (central Colombia, Jamaica) or during spring stopover (northern Colombia; U.S. Gulf of Mexico

Coast in Texas, Louisiana, and Florida; Fig. 2). For detailed site and banding information, see Supporting Information. Individuals that met minimum mass requirements received digitally coded "nanotag" radio transmitters (Lotek Wireless, Ontario, Canada; Table S1). Nanotags were registered with the Motus Wildlife Tracking System, a collaborative network of automated radio telemetry stations distributed across the western hemisphere (motus.org). Motus receivers continuously "listen" for signals on a common frequency and record any tags that pass within the detection radius (up to ~15 km; Taylor et al., 2017), allowing individuals to be tracked with high temporal precision as they migrate. Animal capture and handling adhered to institutional care and use standards and was approved by the Smithsonian Institution Animal Care and Use Committee (#18-09), the University of Massachusetts Amherst Institutional Animal Care and Use Committee (#2015-0019), the University of Saskatchewan Animal Research Ethics Board (#20100084), the University of Southern Mississippi Institutional Animal Care and Use Committee (#17081101), and the Universidad de los Andes animal care and ethics committee - CICUAL (Acta 293, C.FUA_14-016). Research permits were issued by the USGS Bird

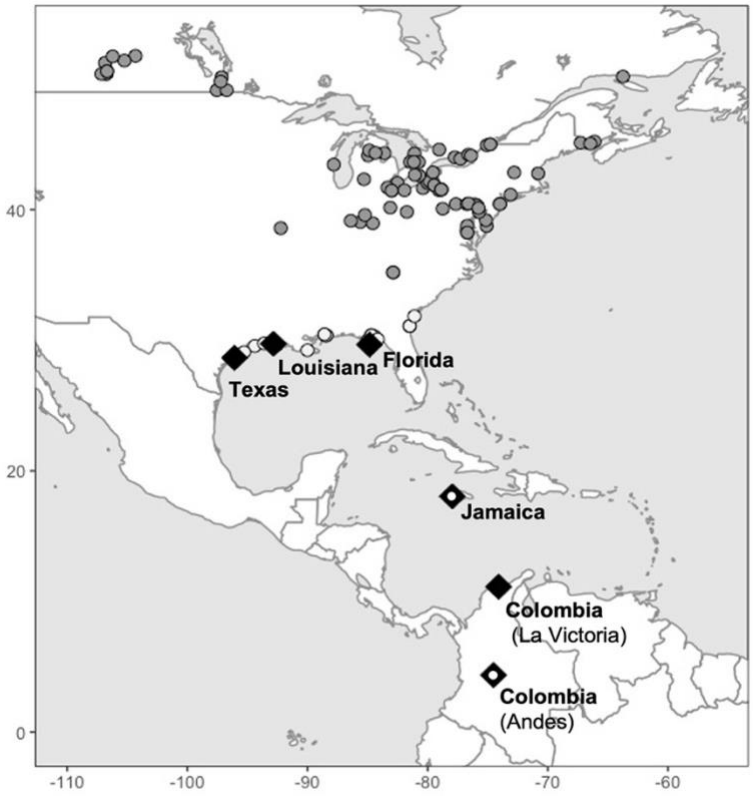


**Figure 2.** Bird tagging locations at spring migration stopover sites (solid black diamonds) and stationary non-breeding sites (black diamonds with dots). Also shown are locations of Motus receivers that detected birds during spring migration through the southern U.S. (white circles) and as they approached their northern breeding locations in the U.S. and Canada (gray circles).

Banding Laboratory (permit numbers 06669, 09700, 24101, and 23979), Texas Parks and Wildlife Department (Scientific Permit SPR-0312-042), The Nature Conservancy Texas Chapter (Scientific Investigation and Collection Permit), Florida Fish and Wildlife Conservation Commission (Permit LSSC-16-00033), Louisiana Department of Wildlife and Fisheries (Scientific Research and Collecting Permits LNHP-18-020 and WDP-19-005), Agencia Nacional de Licencias Ambientales, Colombia (Res. 0597), and Jamaican National Environment and Planning Agency (Ref# 18/27).

We used Motus detections of individual birds as they migrated into temperate North America, primarily along the Gulf Coast in the southeastern U.S., and again as they approached their breeding destinations during the same spring. Thus, each individual bird had paired detection locations and dates in southern and northern portions of North America during the same migration. All Motus detection data were screened and possible false positives removed following recommendations in Crewe et al. (2018); details provided in Supporting Information.

Average **bird migration rate** (km/d), inclusive of flight and stopover, was calculated as the great circle distance between each individual's detection locations divided by the days elapsed between detections. This produced a conservative estimate of the minimum rate at which each bird could have migrated. To validate the use of Motus data for calculating average migration rate, we also estimated flight speeds (m/s) by estimating the total hours spent in flight based on a theoretical 1:7 ratio of time in flight : time on stopover (Hedenström and Alerstam 1997). We then divided distance traveled by estimated hours in flight to obtain a coarse estimate of average flight speed.

**Green wave rate and spring onset timing**

The green wave concept describes the progression of vegetation emergence (spring onset) over time and space at the continental scale. We therefore used **spring onset** (day of year) as a static measure of the green wave's timing of arrival to a location. We calculated the **green wave rate** (km/d) as the distance between bird detection locations divided by the difference in spring onset between them. The green wave rate is thus directly comparable with the average migration rate (km/d) of each individual because it is calculated between the same points on the landscape.

We characterized spring onset with two independent methods based on temperature and remotely-sensed measures of vegetation phenology (Polgar and Primack 2011), using vegetation growth as an indicator of prey available to insectivorous migrants (van Asch and Visser 2007). Satellite-derived remote sensing products, including the normalized difference vegetation index (NDVI), directly measure vegetation greenness, whereas temperature-based metrics such as cumulative growing degree-days record thermal sums as proxies for plant development (Pettorelli et al. 2005, Polgar and Primack 2011, Schwartz et al. 2013). While it was not our intention to formally compare the ability of different phenology estimators to predict songbird migration, we were interested to see if general patterns were consistent between approaches. We discuss the first method of characterizing spring onset in detail below and describe the NDVI-based method in the Supporting Information.

The temperature-based estimate of spring onset, the U.S. National Phenology Network (USA-NPN) Extended Spring Index First Leaf Date, uses growing degree-day thresholds to predict timing of leaf-out across the United States (Schwartz et al. 2013). We used the USA-NPN's product for spring onset day of year for each of the four years in which birds were tracked. Annual first leaf estimates were only available for the continental U.S.; however, many

of the Motus detections in Canada occurred close to the U.S. border. For these individuals, we used the points2nearestcell function in R package rSDM (Rodriguez-Sanchez 2022) to extract values from the closest U.S. cell in the first leaf raster, using 155 km as the maximum distance threshold (n = 24 locations).

**Phenological interval**

The migratory strategy relative to the green wave is determined by the migration rate and the phenological interval along the migration route (Fig. 1). The **phenological interval** is the number of days between a bird's migratory passage and spring onset day of year (Mayor et al. 2017); values are positive when migrating birds arrive at a location after spring onset and negative when they arrive before it (i.e., before the green wave arrives). Animals may maintain a constant phenological interval along the migration route ("Surfing" strategies, with "Leading Edge" surfing signified by a phenological interval of zero and "Trailing" surfing signified by a positive phenological interval). Conversely, phenological interval may decrease along the migration route ("Catching Up" or "Jumping" strategies), corresponding to shorter times between migratory passage and spring onset with increasing latitude. Individuals that "jump" over the green wave switch from a positive phenological interval to a negative one.

**Migration phenology models**

To investigate the effect of green wave rate on bird migration rate, we fitted generalized least squares regressions using the R package nlme (Pinheiro et al. 2020) with bird migration rate (km/d) as the response variable. As predictors, we included green wave rate, species, and time of season (ordinal day that the bird migrated through the southeastern U.S.). To test the hypothesis that the relationship between the green wave rate and migration rate depends on whether a bird is an earlier or later season migrant, we included an interaction term between green wave rate and

time of season. To test our expectation that insectivorous birds use a Surfing - Trailing migration strategy, we fitted linear mixed-effects models with phenological interval as the response variable and detection location (factor with two levels: southern receiver or northern receiver; Fig. 2) as a predictor variable. We also included species (four-level factor) as a fixed effect and individual as a random effect to account for paired observations.

For each question, we fitted separate models for spring onset estimated by the USA-NPN extended spring index of first leaf (hereafter **first leaf spring onset**) and spring onset estimated by vegetation greenness change (hereafter **NDVI spring onset**). We verified model assumptions by visually inspecting residual plots using base R and R package 'performance' (Lüdecke et al. 2021). If residuals showed heteroscedasticity, we evaluated different weights for the variance covariate(s) and selected the optimal variance structure based on AIC values and improvement in residual plots (Zuur et al. 2009, Pinheiro et al. 2020). Collinear predictor variables (VIF >5) were removed. We plotted predictions from fitted models with packages 'visreg', 'ggeffects', and 'ggplot2' (Wickham 2016, Breheny and Burchett 2017, Lüdecke 2018). All analyses were performed using R version 3.6.3 (R Core Team 2020). For model results, we report mean ± SE unless noted otherwise.

In most cases, results were qualitatively similar regardless of which method (first leaf or NDVI) was used to characterize spring phenology. We thus present the results of first leaf spring onset models in detail below, noting differences from NDVI models where they occur, and provide full NDVI and first leaf model results in the Supporting Information (Tables S2 - S5).

## Results

From 2016 - 2019, we tracked 103 individuals during spring migration within North America (Fig. 3a, Table 1). Birds migrated through the U.S. Gulf of Mexico Coast region between 6 April and 30 May and were detected further north, approaching breeding areas, between 29 April and 11 June. Average northward migration rate was fastest in Ovenbirds followed by Gray-cheeked Thrush and Swainson's Thrush, with Northern Waterthrush migrating the slowest (Table 1).

**Table 1.** Spring migration tracking results of four Nearctic-Neotropical songbird species captured at three sites along the U.S. Gulf of Mexico coast, two in Columbia, and one in Jamaica between 2016 - 2019. Migration rates and flight speeds are reported as mean ± SD. Annual variation in migration rate by species is shown in Supporting Information (Fig. S5 – S6).

| **Species** | **n** | **Tagging locations** | **Years tracked** | **Migration rate** (km/d) | **Flight speed** (m/s) |
|---|---|---|---|---|---|
| Swainson's Thrush | 72 | Colombia (Andes), Texas, Louisiana, Florida | 2016 - 2019 | 145 ± 55.6 | 13.4 ± 5.1 |
| Northern Waterthrush | 14 | Louisiana, Florida | 2016 - 2019 | 121 ± 44.6 | 11.2 ± 4.1 |
| Gray-cheeked Thrush | 10 | Colombia (La Victoria, Andes), Florida | 2016 - 2018 | 161 ± 51.2 | 14.9 ± 4.7 |
| Ovenbird | 7 | Jamaica, Texas | 2019 | 236 ±103.0 | 21.9 ± 9.6 |

The range of migration rates of Motus-tracked birds in our study overlapped those reported elsewhere, e.g., approximately 220 km/d including flight and stopover for Gray-cheeked Thrushes migrating between Colombia and the U.S. (range: 88 - 710 km/d, n = 33; Gómez et al., 2017). Comparing our Motus-derived estimates with empirical flight speed measurements provides a useful validation. For example, using our migration rate (km/d) estimates and a theoretical 1:7 flight-to-stopover time ratio, we calculated flight speeds (m/s) for Motus-tracked Swainson's Thrushes to be 13.4 ± 5.1 (mean ± SD, range: 5.6 - 33.3 m/s, n = 72). These are

consistent with direct flight speed measurements of *Catharus* thrushes (e.g., 13.6 - 16.6 m/s, Bowlin 2005; 10.1 m/s, Cochran and Kjos 1985).

In general, the first leaf model predicted spring to occur earlier than the NDVI-based model (Fig. 3c-d). At southeastern sites, annual spring onset day estimated with the first leaf method ranged from 15 January - 3 February (mean: 25 January ± 5.02 days, n = 26 sites). Using NDVI, spring onset estimates were nearly two months later (mean: 20 March ± 6.92 days, range: 11 March - 7 April, n = 16). For the northern sites, which spanned a wider latitudinal range (42.9 - 51.8°N), first leaf spring onset day ranged from 21 February - 2 May (mean: 7 April ± 17.5 days, n = 70) while NDVI spring onset day ranged from 5 April - 19 May (mean: 23 April ± 9.13 days, n = 61).

We predicted that the first leaf green wave rate, a measure of how quickly spring "travels" across the continent, affects how quickly birds migrate within North America. We had expected that the relationship between migration rate and green wave rate would depend on the time of season (day of year) that birds migrated through the southeastern U.S., and this interaction term was important in the full model (green wave rate x time of season: $\chi^2$= 8.22, p = 0.004; Table S2). However, in contrast to our predictions, migration rate of earlier-season birds was negatively related to the green wave rate, whereas for later-season birds there was a positive relationship (Fig. S2a). On further exploration we found that four observations (two Swainson's Thrushes and two Northern Waterthrushes), corresponding to very high green wave rate values, were driving the unexpected early-season interaction. All individuals were detected at the same pair of Motus receivers in 2018, meaning that we calculated the same green wave rate value for all four birds. When the model was re-fitted omitting these data, the interaction term was no longer significant ($\chi^2$ = 3.02, p = 0.083, df = 1), nor was the green wave rate. Migration rate was

positively related to time of season in this refitted model ($\chi^2 = 37.21$, $p < 0.0001$, df = 1; Fig. S2b), irrespective of green wave rate.

Birds appeared to catch up to the green wave as they traveled across North America. All birds arrived after first leaf spring onset in the southeastern U.S. (south phenological interval = 102 ± 1.1 days, range: 68 - 119, n = 92) and were detected fewer days after spring onset as they migrated northwards (north phenological interval = 45 ± 1.8 days, range: 6 - 91, n = 92). Bird detection location (north or south) was an important predictor of phenological interval ($\chi^2$ = 227.31, $p < 0.0001$, df = 1). Northern phenological interval was substantially smaller than southern phenological interval, indicating that birds migrated faster than the green wave and were "catching up" to it as they approached their breeding destinations. Swainson's Thrushes (n = 64) migrated through the U.S. approximately 104 ± 1.2 days after spring onset in the south and 46 ± 2.0 days after spring onset in the north (Fig. 3d). Northern Waterthrushes (n = 12) migrated earlier than other species through both southern and northern regions (Fig. 3d, Table S4).

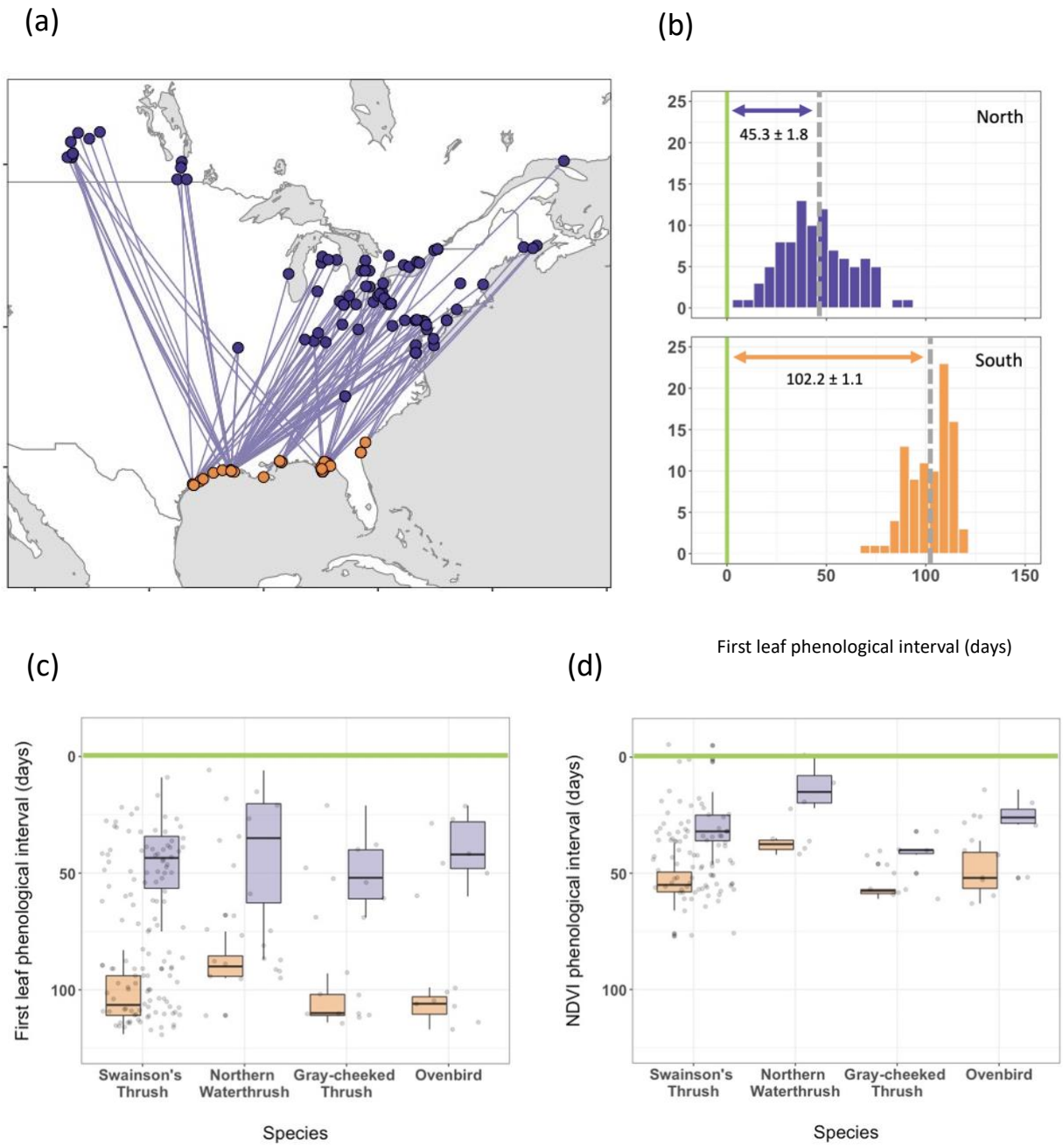


**Figure 3.** (a) Locations of south (orange) and north (purple) bird detection sites with lines connecting each individual's detections. Note that track lines denote the shortest distance between points and do not necessarily represent a bird's actual migration route. (b) Frequencies of phenological intervals (bird migration day relative to local spring onset day of year, here estimated using the first leaf spring index) for birds migrating through the southern U.S. (bottom, orange) versus further north in the U.S. and Canada (top, purple). Dashed vertical line represents the mean phenological interval at south and north sites. Spring onset day of year (green line) has been centered at 0 so that a positive interval means birds arrive after spring onset and a negative interval means birds arrive before it. A smaller positive phenological interval indicates that individuals migrate through an area fewer days after local spring onset and therefore likely experience an earlier stage of spring phenology than individuals arriving later. Species-specific differences in phenological interval using (c) first leaf out and (d) NDVI in the south (orange) and the north (purple). Note position of y-axis scale with 0, representing spring onset, at the top.

## Discussion

Our study leveraged the power of the Motus wildlife tracking system, a unique collaborative network for studying animal movement, to track individual songbirds from multiple non-breeding and stopover sites as they migrated through North America in spring. Unlike many species of herbivores, songbirds in our study did not surf at the green wave's leading edge, nor did they surf behind the green wave by timing their migrations to arrive a consistent number of days after spring onset across their routes. Instead, all birds arrived in the southern U.S. well after spring onset but traveled substantially faster than the green wave while migrating through the U.S. and Canada. Consequently, individuals caught up to the green wave as they approached their breeding grounds, migrating through northern areas closer to the time of local spring onset (Fig. 3). This pattern was consistent whether we defined spring onset using first leaf or NDVI. Because the first leaf model estimates spring onset to occur earlier than the NDVI model, birds were detected "further behind" the first leaf green wave than the NDVI green wave at both detection points. Regardless of method, birds in our study appeared to follow a catching-up pattern within temperate North America.

What is the advantage of the observed catching up strategy? It may imply that no single stage of spring vegetation phenology (corresponding to food availability or quality) is sufficiently beneficial or reliable for songbirds to track a specific phenophase throughout the entire migratory period, as occurs with surfing populations (Armstrong et al. 2016). For generalist insectivore species, resource waves may be composed of a variety of prey species with their own distinct phenologies that are in turn dependent on complex vegetation communities, meaning that there may be successive overlapping resource waves available to support energetic needs *en route* (Armstrong et al. 2016, Donnelly et al. 2017). Songbirds exploit broader niches

during migration, using a wider variety of food sources, foraging behaviors, and habitat types than during non-migratory periods (Parrish 2000, Zuckerberg et al. 2016). Songbirds may therefore be less constrained to follow a particular phenophase than commonly-studied herbivores migrating through less vegetatively complex ecosystems in the arctic and subarctic (e.g., van der Graaf et al. 2006).

We did not find evidence for our hypothesis that migration rate of early-migrating individuals is more sensitive to the green wave than later-migrating individuals. Instead, we observed a somewhat puzzling pattern of early birds migrating more slowly as the green wave rate increased, and later birds migrating faster as expected. However, this pattern was driven by a few observations of early individuals with very high green wave rates and the interaction was no longer supported once these values were dropped. In the refitted model (Fig. S2b), the green wave no longer influenced migration rate and individuals migrating later in the season traveled faster than earlier-migrating conspecifics (Fig. S4), presumably because of increased time pressure to reach the breeding grounds (Jenni and Schaub 2003a), or the potential benefits of migrating later and faster (Gonzalez et al. 2021).

Because our data did not allow us to identify the breeding locations of the birds in our sample, we are unable to infer how proximity to the destination affected their migration rate and timing. In general, migration rate increases as birds approach their breeding areas (González et al. 2020), primarily though reductions in stopover duration (Schmaljohann et al. 2017). It is possible that synchrony between bird migration and spring onset increases with proximity to the breeding grounds, when it would presumably be the most important for successful reproduction (Smith and Moore 2005a). By the time long-distance migrants reach the southeastern U.S., spring phenology is well advanced (Ault et al. 2015) and there is little danger of food limitation

(Zenzal, *unpublished data*). However, because we found migration rate was faster than the green wave rate, the risk of mistiming may increase as birds travel northward. At some point, it may become more important for birds to fine-tune migration pace to avoid "overshooting" favorable phenological conditions (Youngflesh et al. 2021) and possibly incurring a survival cost.

Correlations in environmental conditions along the route can substantially influence migration timing because information about phenology at the next stopover site or destination is more reliable when conditions are correlated (Kölzsch et al. 2015, Bauer et al. 2020, Abrahms et al. 2021). We did not measure the degree of phenological predictability in our study and thus cannot assess how well spring onset on the Gulf Coast predicts spring onset elsewhere *en route*. However, due to spatial correlation, birds that have a shorter distance to travel within North America probably obtain more valuable information about phenology on their breeding grounds during Gulf Coast stopovers than longer distance migrants, and use this to time migratory initiation and departures (Zenzal Jr. et al. In Press). In support of this, short-distance migrants generally show greater sensitivity and adjustments to migration timing in response to phenological changes than long-distance migrants (Miller-Rushing et al. 2008, Hurlbert and Liang 2012, Youngflesh et al. 2021).

Individuals from different populations of many species stop over on the U.S. Gulf Coast during spring migration (Langin et al. 2009), and birds in our sample may therefore represent a mixture of populations with different breeding and non-breeding areas (Cohen et al. 2017, Zenzal Jr. et al. 2018a, Cohen et al. 2019). Conditions in the non-breeding range can vary signficiantly between years and can affect timing of departure from stationary areas and stopover sites, fueling rates, and birds' overall speed and physical condition during migration (Studds and Marra 2011, González-Prieto and Hobson 2013, Paxton et al. 2014, Gómez et al. 2017, but see

(González et al. 2020, Dossman et al. 2022). With the exception of birds tagged in central Colombia and Jamaica, we could not tell where individuals in our study spent the stationary non-breeding season, and hence could not incorporate any carryover effects resulting from exposure to different environmental conditions prior to detection in the southeastern U.S. Similarly, birds may time their migrations to match expected conditions at their breeding destinations; individuals we tracked were detected across a range of longitudes after departing the Gulf, but we have no *a priori* knowledge of their breeding areas. Both species- and individual-level differences in migration rate could be partly explained by differences in breeding destination and total distances traveled (Dossman et al. 2022).

**Data Limitations and Future Work**

Determining if songbirds adjust migration timing to the green wave may be sensitive to the data types, spatial and temporal scales, and modeling approaches used to characterize environmental and migration phenology (Schwartz et al. 2013, White et al. 2014). For example, Kelly et al. (2016) found that first leaf date was positively correlated with spring songbird migration in eastern North America estimated from eBird and weather radar data, yet NDVI phenology estimates did not explain migration timing. In contrast, using eBird observations and the Enhanced Vegetation Index, La Sorte and Graham (2021) found that many North American species synchronized their migrations with vegetation greenness throughout the year.

Discrepancies in the ability of different spring onset metrics to predict animal migration phenology may be partly explained by differences in the biological phenomena that each approach measures. The NDVI quantifies changing vegetation greenness and thus directly reflects food available to herbivores while indirectly measuring food for insectivores (such as songbirds that eat herbivorous caterpillars). In contrast, the first leaf spring index predicts leaf

development based on thermal sums (Polgar and Primack 2011). Temperature influences caterpillar emergence and activity both directly, because arthropod development is linked to temperature, and indirectly, by promoting the development of leaves upon which caterpillars feed. In general, dates of spring onset derived from temperature-based models and remotely-sensed vegetation indices are broadly correlated (Zurita-Milla et al. 2020). Accordingly, we found similar patterns in migration rate and timing regardless of whether we characterized spring using temperature-based first leaf models or satellite-derived NDVI models, despite absolute differences in estimated spring onset day.

Our study made a number of simplifying assumptions. Bird tracking data consisted of "snapshot" detections at two points along each individual's migratory journey. This represents an important but incomplete segment of the migratory track; for example, if additional birds ultimately jumped over the green wave at higher latitudes, we would be unable to distinguish this from a catching up pattern because of the limited number of Motus receivers operating further north. As discussed, environmental conditions at the endpoints of the track – the non-breeding departure location and the breeding destination – and at stopover sites throughout the Americas also influence migration rate and timing (Studds and Marra 2011, González-Prieto and Hobson 2013). Another limitation was our inability to investigate potentially important heterogeneity in the progression of migration and vegetation phenology between detection locations and through time (Ahola et al. 2004). Additional detections would have allowed us to see if migration rate and green wave rate differed between track segments, perhaps reflecting differences in stopover site phenology and quality that can vary between years. Furthermore, our sample size was too small to model effects of factors such as wind direction, age, and sex, which can be important

determinants of migration rate and timing (Morbey et al. 2018, McKinnon and Love 2018, Dossman et al. 2022)

Despite its limitations, the temporal precision of Motus data is excellent, especially compared to other technology currently available for tracking small songbirds (McKinnon and Love 2018). We also confirmed that Motus can be used to derive plausible estimates of flight speed and migration rate. Establishing additional receiver stations at stopover sites south of the Gulf of Mexico and throughout migrants' non-breeding ranges would be extremely valuable for understanding migratory connectivity and *en route* variation in stopover ecology and timing (Gómez et al. 2017, Bayly et al. 2018). Expanding the network northward and westward could clarify connectivity and drivers of timing for populations that breed at high latitudes or traverse wide longitudinal spans during migration (Ruegg et al. 2006). Complementary approaches, such as sex identification and assigning individuals to breeding and wintering populations using stable isotopes and genetic markers in feather samples (Hobson et al. 2014, Ruegg et al. 2014), can help fill in the gaps as the Motus network continues to grow.

## Conclusions

As climate change affects the timing of organisms' life history events, animals may grow increasingly out of sync with the phenology of resources in their environments. Migratory birds are flexible enough to adjust to novel conditions *en route* and hence may be expected to cope with changing conditions better than other organisms (Charmantier and Gienapp 2014). However, long-distance migrants may be unable to keep pace with rapid changes beyond a certain point and could suffer negative consequences (Miller-Rushing et al. 2008, Carey 2009, Connare and Islam 2022). The catching up strategy that we found in songbirds migrating through eastern North America may indicate that they can exploit a range of phenological phases during

migration, which we hypothesize corresponds to a shifting variety of arthropod food sources *en route.* In effect, these species could be considered generalists rather than specialists with regards to resource phenology during this phase of their life cycle. Flexibility and breadth in diet could help buffer songbirds from harmful effects of climate change-induced phenological mismatches during migration, but additional tracking of individual migrants is necessary to clarify the adaptive value of this strategy and if it is maintained as birds near their destinations.

**Acknowledgments**

Steven Guinn generously provided the NDVI spring onset data. Andrew Elmore offered invaluable assistance with NDVI analyses. Members of the UMCES Animal Migration Research Group, especially Megan Massa, gave helpful feedback on the figures. Frank R. Moore, Wylie C. Barrow Jr., Lori A. Randall, Lily Calderón, Jaclyn Smolinsky, and Michael Seymour provided essential support in Louisiana. We are grateful for the field technicians who assisted with data collection and for the organizations and individuals who provided permissions and site access, including The Nature Conservancy Louisiana and Texas (Clive Runnells Family Mad Island Marsh Preserve), the Nunez and Hollister families in Louisiana, and the Apalachicola National Estuarine Research Reserve in Florida. The UMCES Appalachian Laboratory and the University of Maryland Marine, Estuarine, and Environmental Science program provided support to CEN. TJZ was supported by NA17NOS4510092 during the fieldwork portion of this project. Fieldwork in central Colombia was funded by an operating grant to Keith Hobson from Environment and Climate Change Canada, and by Birds Canada. Fieldwork in Louisiana was supported by the U.S. Agency for International Development (AID-0AA-A-11-00012), NOAA RESTORE Act Science Program (NA17NOS4510092), and the Louisiana Department of Wildlife and Fisheries' Rockefeller Trust Fund, a statutory dedicated fund for research and

management. Fieldwork in Florida was supported by National Science Foundation IOS-1656726, the American Ornithologists' Union, and the Wilson Ornithological Society. Fieldwork in Jamaica was funded by a Cornell Lab of Ornithology Athena grant to BCD, Smithsonian Institution James Bond Endowment Fund to BCD and PPM, and an NSF LTREB (#1242584) grant to PPM. We further thank Stu Mackenzie, the Canadian Wildlife Service, and the teams of researchers and volunteers who are helping to grow the Motus network. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

**Conflict of Interest**

The authors have no conflicts of interests to declare.

**Author Contributions**

CEN and EBC conceived of the project and developed hypotheses. CEN conducted the analyses and wrote the manuscript. PPM, TJZ, SAC, BCD, ARG, CG, AMG, MGR, SAH, JM, PLV, and EBC conducted fieldwork and contributed Motus data. PPM and SAH provided financial support. All authors reviewed and provided feedback on the manuscript.

**Data Availability Statement**

Data will be available from the Dryad Digital Repository and Motus.org.

## Chapter 2 Supporting Information

Songbirds in North America catch the green wave, but not by surfing. C.E. Nemes, P.P. Marra, T.J. Zenzal Jr., S.A. Collins, B.C. Dossman, A.R. Gerson, C. Gómez, A.M. González, M. Gutierrez Ramirez, S.A. Hamer, J. Marty, P.L. Vasseur, and E.B. Cohen

### Supplemental Methods – Motus Tracking

*Study System*

The four species tagged in this study are primarily insectivorous and associated with the forest understory during migration (Billerman et al. 2020). They breed across forested regions of eastern North America and spend the stationary non-breeding period in South America (Swainson's and Gray-cheeked Thrush; Mack & Yong, 2020; Whitaker et al., 2020) or Central America and the Caribbean (Northern Waterthrush and Ovenbird; Porneluzi et al., 2020; Whitaker & Eaton, 2020). Stationary non-breeding capture locations included the Eastern Andes of Colombia in shade coffee or secondary forest habitat (4° 21' N, -74° 31' W; (González et al. 2020) or in Jamaica at Font Hill Nature Preserve, St. Elizabeth Parish (18° 2' N, -77° 56' W; (Powell et al. 2021). Spring stopover capture locations included La Victoria in the Sierra Nevada de Santa Marta mountains of northern Colombia (11° 7' N, -74° 5' W; Gómez et al., 2017) and three sites on the northern Gulf of Mexico Coast: chenier forest (i.e., oak-covered remnant beach ridges) on Grand Chenier of Cameron Parish, Louisiana (29° 4' N, -92° 5' W; Holcomb et al., 2015); coastal scrub forest at The Nature Conservancy's Clive Runnells Family Mad Island Marsh Preserve in Matagorda County, Texas (28° 4' N, -96° 6′ W; (Cohen et al. 2019); and scrub forest on the barrier island of St. George in Apalachicola National Estuarine Research Reserve in Franklin County, Florida (29° 4' N, -84° 5′ W; Gutierrez Ramirez et al., 2022; Figure 2).

*Tagging*

Birds were captured using mist nets and individuals meeting minimum mass requirements were outfitted with Lotek digitally encoded "nanotag" radio transmitters (Table S1) broadcasting at 166.380 MHz, currently the most common frequency used by receivers in the Motus network in the western hemisphere (Taylor et al. 2017). Nanotags were affixed using a leg-loop harness (Rappole and Tipton 1991, Streby et al. 2015) for all species except Northern Waterthrushes tagged in Louisiana, for which adhesives were used to affix nanotags to the dorsum using a modified version of Raim (1978) (for details, see (Smolinsky et al. 2013, Zenzal Jr. et al. 2018b). The combined weight of nanotag and harness or adhesive did not exceed 5% of the bird's mass. While it is possible that transmitters could reduce migration rate, researchers have found no difference in rates of birds tagged with different transmitter sizes (González et al. 2020), indicating that effects are likely minimal.

*Motus Data Filtration*

We followed recommendations in the Motus R Book (Crewe et al. 2018) to access and filter detections of tagged birds using the R package 'motus' (Birds Canada 2022). After downloading the complete detection databases for birds tagged at the six locations in this study, we subsetted to detections occurring between 1 January and 15 June of the year the bird was tagged. While many birds commence breeding before 15 June in much of their range, we did not know the breeding destinations of birds in our study and indiviuals breeding at very high latitudes might still be detected on migration through the U.S. and Canada during early June (Mack and Yong 2020, Whitaker et al. 2020).

Groups of tag detections at a single antenna of a receiver are called "runs." Short runs (run lengths of $\leq$4 for "quiet" receiver sites and $\geq$5 at "noisy" receiver sites) have a high probability of being false positive detections; we removed these by omitting rows with a "0" in

the motusFilter column (Crewe et al. 2018). Because this likely omitted some true detections, we also used the filterByActivity() function to compare three different thresholds (strict, standard, and relaxed). The "standard" filter corresponded to the default motusFilter thresholds, with the "relaxed" filter allowing shorter run lengths and the "strict" filter keeping only longer runs. We compared detections of each tag under all three filtration levels to identify any discrepancies and examine them in more detail.

To determine the validity of each detection, we used plots of tag signal strength and receiver location over time (Crewe et al., 2018; Fig. S1) in combination with species' biology. For example, if a bird was first detected at one northern receiver and then several days later at a receiver to the south (unlikely behavior for a bird migrating generally northward in spring), we examined plots of each detection to determine if it occurred at a biologically plausible time, location, and pattern. In general, the default motusFilter thesholds performed well, although false positive detections occasionally occurred (identified by unrealistic flight paths between receivers, detections outside of the known range of the species, etc.) When in doubt about a detection's validity, we took a conservative approach and omitted it from our analysis.

When individuals were detected at more than one receiver in the southern U.S., we only used the time stamp and receiver location of the final detection, which typically corresponded to nocturnal departure flight (verified by plotting tag signal strength; Crewe et al., 2018). Because we could not calculate minimum stopover duration for all individuals (only those that were captured and tagged at the three Gulf Coast sites) we chose the date of the final southern detection to facilitate comparison across all birds. We assumed indviduals that were detected departing from the Gulf Coast late in the season had also arrived on the Gulf Coast late. For individuals detected at more than one northern receiver, we only used the time stamp and

receiver location of the first detection. In most cases, multiple detections occurred at receivers in relatively close proximity to one another. Distance estimates are based on receiver location and not the bird's location, which could be anywhere within the receiver's 20 - 30km total detection diameter (Taylor et al. 2017), and hence migration speeds may be inaccurate and implausibly high when estimated for receivers less than 100km apart (motus.org). Migration rates and flight speeds were thus only calculated when detections occurred between receivers that were at least 150km apart to minimize the effect of positional uncertainty on distance estimates.

The number of active Motus receiver stations varied between years of our study but has been increasing as the network expands. Motus maintains a publicly available interactive map of historically and currently active receivers on its website (https://motus.org/data/receiversMap).

**Table S1.** Lotek nanotag models, model weights (without harness or adhesive), species, deployment locations, and years used.

| Lotek Tag Model | Weight | Species | Location | Years |
|---|---|---|---|---|
| NTQB-2 | 0.35g | Swainson's Thrush, Gray-cheeked Thrush, Ovenbird, Northern Waterthrush | Colombia (Andes, La Victoria), Texas, Jamaica, Florida | 2015 - 2019 |
| NTQB2-2 | 0.32g | Swainson's Thrush, Northern Waterthrush | Texas, Louisiana | 2018, 2019 |
| NTQB-3-2 | 0.67g | Swainson's Thrush, Gray-cheeked Thrush | Colombia (Andes), Florida | 2015 - 2018 |
| NTQB2-3-2 | 0.66g | Swainson's Thrush, Gray-cheeked Thrush | Louisiana, Florida | 2018, 2019 |
| NTQB-4-2 | 0.9g | Swainson's Thrush | Colombia (Andes) | 2016 |

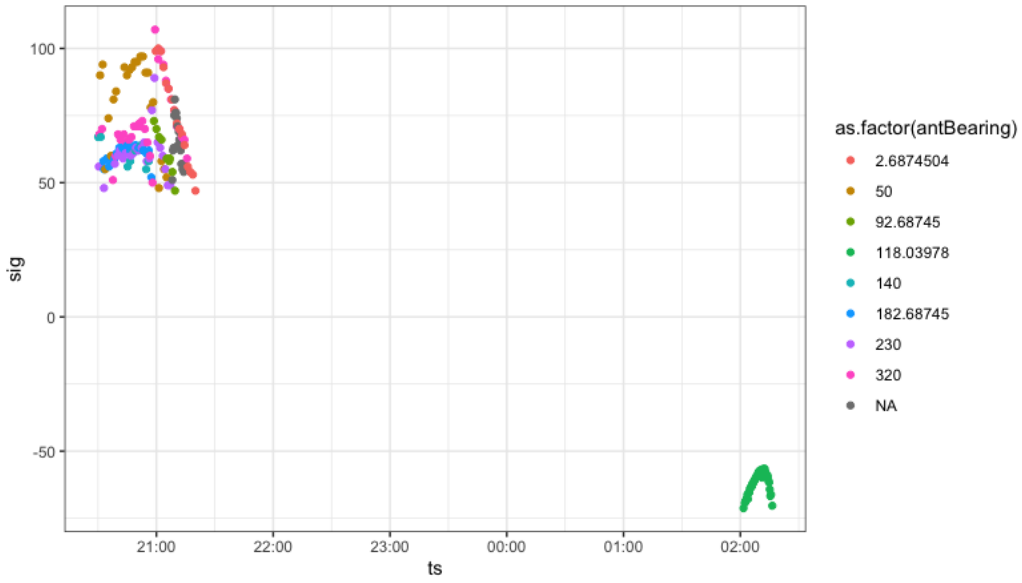


**Figure S1**. Example detection patterns of a nanotagged bird during nocturnal flight, as detected by several Motus automated telemetry receivers. The x-axis shows the time stamp in seconds (UTC; local time is UTC -5) and the y-axis shows tag signal strength; dots represent detections of the bird's tag signal with colors corresponding to the antenna with which it was detected. On the left, the cluster of signal pulses at ~21:00 occurred when the bird was detected simultaneously by multiple receivers (each bearing 3-4 antennas). On the right (~02:00), the bird was detected passing by a Motus receiver with a single antenna. Signal strength rises and falls in a characteristic "rainbow" or arc pattern as the bird approaches and then flies past a given receiver; together with the time stamp, this signifies a nocturnal flyby detection rather than a stopover.

**Supplemental Methods – NDVI Spring Onset Analysis**

*Methods*

To estimate spring onset using satellite imagery, we obtained NASA MODIS NDVI surface reflectance images (MOD09A1.006 Terra Surface Reflectance 8-Day Global - 500m resolution) from years 2000 - 2019 within a 10 km buffer around each bird detection location, masked out pixels containing clouds, ice, or snow with the MODIS QA band, and used the MCD12Q1.006 MODIS Land Cover Type Yearly Global (500m resolution) product to mask non-forest pixels before calculating NDVI for the remaining images.

Following Elmore et al. (2012), we stacked the time series for each location by day of year and fitted a double logistic curve to model vegetation growth. The model produced estimates of **expected NDVI spring onset**, defined as the day on which vegetation greenness is predicted to change most rapidly for each detection location (Pettorelli et al. 2005, Elmore et al. 2012). We then used the parameters from the phenology curve fitted to the stacked NDVI time series at each site to predict the day of year on which an observed NDVI value was most likely (Melaas et al. 2013, Elmore et al. 2016). The difference between the fitted and observed NDVI values (residual) each year is the estimated **NDVI spring onset anomaly** (i.e., the number of days earlier or later than expected that spring onset actually occurred (Melaas et al. 2013). To calculate the **actual NDVI spring onset day** for each year, we added the yearly spring onset anomaly to the expected (i.e., long-term average) NDVI spring onset day. In instances when the model was unable to reliably estimate spring phenology at locations with too few forested pixels within the specified buffer, we used data from the closest coordinates where parameter estimates were successfully estimated, typically within 20 km and no more than 90 km. Using the actual NDVI spring onset day of year, we calculated the **NDVI green wave rate** and **NDVI**

**phenological interval** as described in the main text. All methods for modeling bird migration rate and timing using the NDVI spring onset estimates are the same as described for the first leaf spring onset estimates in the main text.

*Results*

The NDVI model estimated average spring onset at both detection locations for 89 individuals but was only able to estimate actual NDVI spring onset for a subset of 63 individuals due to cloud cover interference or insufficient forest extent. The mean 15-year average NDVI spring onset day in the south was similar at 12 March ± 20.3 days (range: 5 February - 9 April, n = 26 sites). The mean 15-year average NDVI spring onset day was 25 April ± 8.0 days (range: 9 April - 22 May, n = 67 sites). Actual NDVI spring onset day estimates, listed in the main text Results section, were similar to expected NDVI spring onset estimates (averaged over the 15 years prior to the year in which the individual was tracked.)

For the migration rate model using NDVI green wave rate estimates, no predictors were important in the full model (Table S2a). However, when we dropped the NDVI green wave rate x time of season interaction term, green wave rate and time of season were both significant and positively related to migration rate in the reduced model (Table S2b), indicating that birds migrated faster later in the season and when the NDVI green wave rate was faster.

As with the first leaf green wave, when using NDVI to estimate spring onset, we found that birds increasingly caught up to the NDVI green wave as they migrated through the U.S. and Canada (Fig. 3e, Table S4). Birds arrived in the southern U.S. an average of 53 ± 1.1 days after actual NDVI spring onset (range: 35 to 77, n = 63) but caught up to the green wave as they migrated and were detected 29 ± 1.5 days (range: -5 to 52 days) after spring onset in the north. Two individuals, a Northern Waterthrush and a Swainson’s Thrush, appeared to overtake (i.e.,

"jump") the green wave and were detected several days before annual NDVI spring onset (north phenological intervals of -1 and -5 days, respectively).

**Supplemental Results**

In the sections below we present results for model predictions for all model groups. Migration rate and migration strategy have two associated models each: (1) actual spring onset estimated with first leaf spring index and (2) actual spring onset estimated with NDVI. Tables were exported with the assistance of R package sjPlot (Lüdecke 2022). For all tables, we report $\beta$ coefficient estimates with 95% confidence intervals, Wald t, and p-values.

**Supplemental Results: Migration rate vs. first leaf green wave rate**

**Table S2.** Parameter estimates from the generalized least squares regression model for migration rate using first leaf to estimate spring onset and calculate the rate of the green wave. The reference level for species is Swainson's Thrush. Residual plots from the initial model indicated heteroscedasticity, so we used a combination variance function in the R package nlme (Pinheiro et al. 2020) to allow variance to differ by species (varIdent(form = ~1|species)) and increase with time of season (varPower(form = ~detection day (south)).

| *Predictors* | *β (95% CI)* | *t* | *p* |
|---|---|---|---|
| Intercept | 257.11<br>(-110.68, 624.89) | 1.39 | 0.168 |
| Time of season | -1.12<br>(-4.20, 1.96) | -0.72 | 0.472 |
| Green wave rate (first leaf) | -20.85<br>(-34.56, -7.14) | -3.02 | 0.003 |
| Species: Northern Waterthrush | 36.26<br>(10.50, 62.03) | 2.80 | 0.006 |
| Species: Gray-cheeked Thrush | -14.97<br>(-39.54, 9.60) | -1.21 | 0.229 |
| Species: Ovenbird | 96.20<br>(21.47, 170.93) | 2.56 | 0.012 |

| | | | |
|---|---|---|---|
| Time of season * Green wave rate | 0.17 (0.06, 0.29) | 2.95 | 0.004 |
| Observations | 92 | | |
| $R^2$ | 0.422 | | |

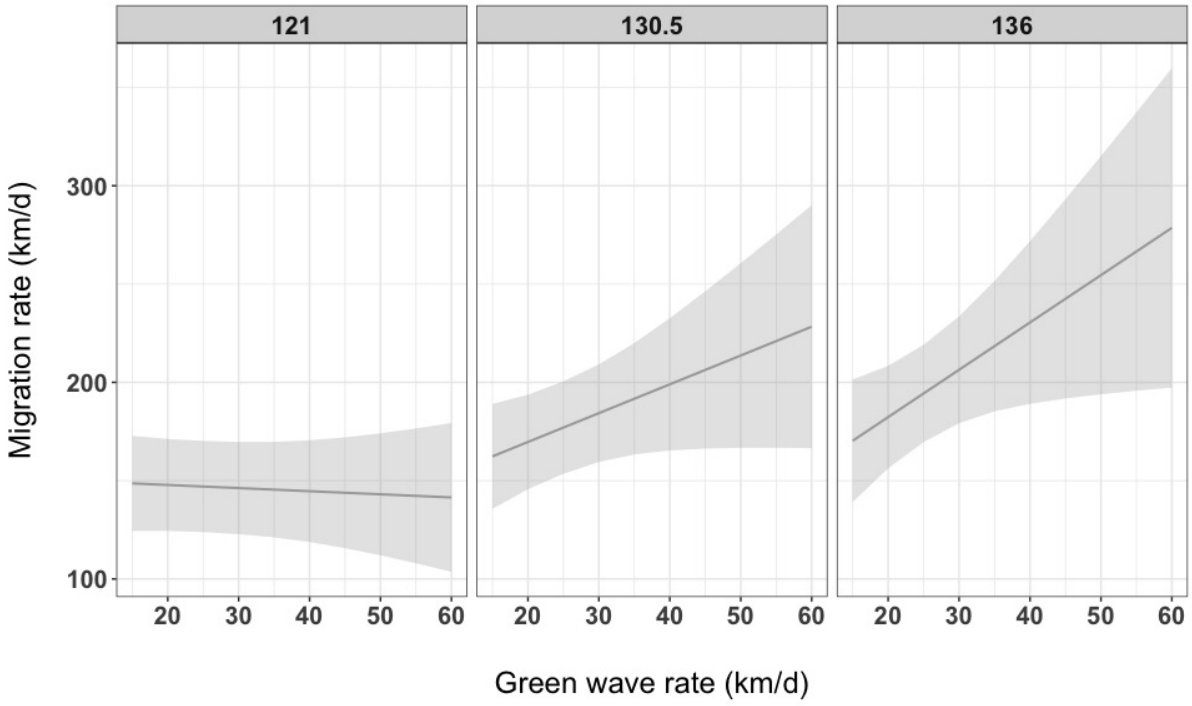


**Fig S2a.** Predictions from the full first leaf green wave rate model. The relationship between migration rate and the green wave depends on time of season (day of year) that birds migrated through the southern U.S. Migration rates of earlier birds (first quartile, corresponding to day of year = 121 (April 30)) exhibiting a negative relationship to green wave rate. Birds migrating through in the middle of the season (median, day of year = 130.5 (May 10)) and later in the season (fourth quartile, day of year = 136 (May 16)) migrated faster as the green wave rate increased. Note that time of season was a continuous variable in our model but is plotted in three groups here to aid interpretation of the interaction between continuous predictors.

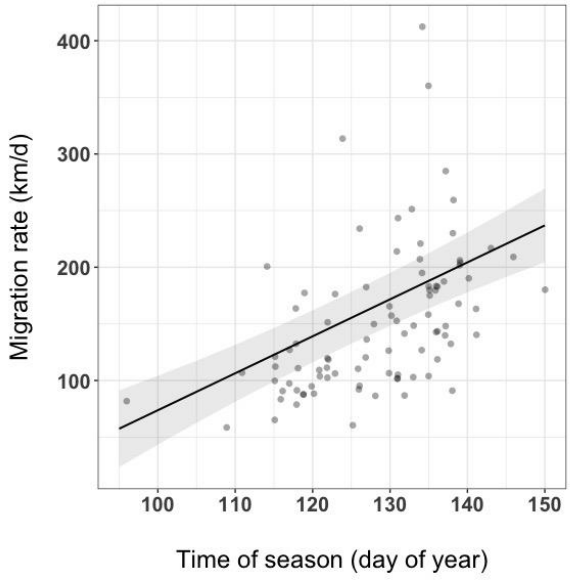


**Fig S2b.** Predicted relationship between time of season and migration rate when the interaction term was dropped from the full model. In the refitted model, migration rate is no longer related to green wave rate and depends on time of season of bird passage through the southern U.S., with late-migrating birds traveling faster than early ones.

**Supplemental Results: Migration rate vs. NDVI green wave rate**

**Table S3a.** Parameter estimates from the full generalized least squares regression model for migration rate using NDVI to estimate spring onset and calculate the rate of the green wave. The reference level for species is Swainson's Thrush. Residual plots from the initial model indicated heteroscedasticity, so we used a combination variance function in the R package nlme (Pinheiro et al. 2020) to allow variance to differ by species (varIdent(form = ~1|species)) and increase with green wave rate (varFixed(form = ~ NDVI green wave rate)).

| *Predictors* | *β (95% CI)* | *t* | *p* |
|---|---|---|---|
| Intercept | -172.31<br>(-1035.99, 691.37) | -0.40 | 0.691 |
| Time of season | 1.97<br>(-4.42, 8.36) | 0.62 | 0.539 |
| NDVI green wave rate | -2.88<br>(-23.45, 17.69) | -0.28 | 0.780 |

| | | | |
|---|---|---|---|
| Species: Northern Waterthrush | 16.58<br>(-34.72, 67.87) | 0.65 | 0.520 |
| Species: Gray-cheeked Thrush | -26.10<br>(-64.58, 12.39) | -1.36 | 0.180 |
| Species: Ovenbird | 93.78<br>(3.69 – 183.86) | 2.09 | 0.042 |
| Time of season * NDVI green wave rate | 0.03<br>(-0.12, 0.18) | 0.42 | 0.674 |
| Observations | 63 | | |
| $R^2$ | 0.352 | | |

**Table S3b.** Parameter estimates from the reduced generalized least squares regression model for migration rate using NDVI green wave rate with the interaction term dropped from the full model. The reference level for species is Swainson's Thrush. Residual plots from the initial model indicated heteroscedasticity, so we used a combination variance function in the R package nlme (Pinheiro et al. 2020) to allow variance to differ by species (varIdent(form = ~1|species)) and increase with green wave rate (varFixed(form = ~ NDVI green wave rate)).

| *Predictors* | *β (95% CI)* | *t* | *p* |
|---|---|---|---|
| Intercept | -351.82<br>(-562.66, -140.98) | -3.34 | 0.001 |
| Time of season | 3.30<br>(1.64, 4.95) | 3.98 | <0.001 |
| NDVI green wave rate | 1.46<br>(0.46, 2.46) | 2.93 | 0.005 |
| Species: Northern Waterthrush | 16.74<br>(-32.59, 66.07) | 0.68 | 0.500 |
| Species: Gray-cheeked Thrush | -23.71<br>(-59.74, 12.32) | -1.32 | 0.193 |
| Species: Ovenbird | 92.49<br>(2.47, 182.50) | 2.06 | 0.044 |
| Observations | 63 | | |
| $R^2$ | 0.351 | | |

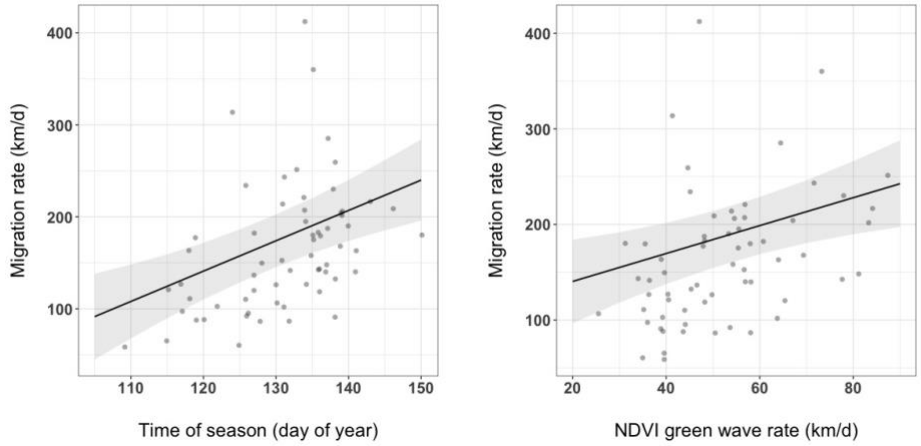


**Figure S3.** Predictions from the reduced NDVI green wave rate model with interaction term dropped, showing positive effects of (a) time of season and (b) NDVI green wave rate on bird migration rate.

**Supplemental Results: Migration strategy (first leaf spring onset)**

**Table S4.** Parameter coefficient estimates of the linear mixed-effects model for phenological interval (bird migration passage day of year relative to first leaf spring onset day of year). Swainson's Thrush and southern receiver are the reference levels, so parameter estimates refer to the three other species and northern receiver. Individual ID was treated as a random intercept (variance component estimates ± SD: 6.83 ± 6.59). Due to heterogeneity of variance between receivers, we allowed within-group errors to have unequal variance by using model weights (varIdent(form = ~1|receiver)) in R package nlme (Pinheiro et al. 2020).

| *Predictors* | *β (95% CI)* | *t* | *p* |
|---|---|---|---|
| Intercept | 103.44<br>(101.11, 105.77) | 86.93 | <0.001 |
| Receiver: North | -56.93<br>(-60.60, -53.27) | -30.41 | <0.001 |
| Species: Northern Waterthrush | -13.24<br>(-18.97, -7.51) | -4.53 | <0.001 |
| Species: Gray-cheeked Thrush | 3.68<br>(-2.80, 10.16) | 1.11 | 0.269 |
| Species: Ovenbird | 2.07<br>(-5.18, 9.32) | 0.56 | 0.577 |

| **Random Effects** | |
|---|---|
| $\sigma^2$ | 43.40 |
| $\tau_{00\ motusTagID}$ | 46.58 |
| $N_{\ motusTagID}$ | 92 |
| Observations | 184 |
| Marginal $R^2$ | 0.951 |

**Supplemental Results: Migration strategy (NDVI spring onset)**

**Table S5.** Parameter coefficient estimates of the linear mixed-effects model for phenological interval (bird migration passage day of year relative to NDVI spring onset day of year). Swainson's Thrush and southern receiver are the reference levels. Individual ID was treated as a random intercept (variance component estimates ± SD: 6.55 ± 4.62).

| | **Phenological interval** | | |
|---|---|---|---|
| *Predictors* | *β (95% CI)* | *t* | *p* |
| Intercept | 53.93<br>(51.59, 56.27) | 46.08 | **<0.001** |
| Receiver: North | -23.37<br>(-25.83, -20.90) | -18.96 | **<0.001** |
| Species: Gray-cheeked Thrush | 4.12<br>(-2.58, 10.82) | 1.23 | 0.223 |
| Species: Ovenbird | -4.13<br>(-10.40, 2.13) | -1.32 | 0.192 |
| Species: Northern Waterthrush | -16.35<br>(-24.40, -8.30) | -4.07 | **<0.001** |
| **Random Effects** | | | |
| $\sigma^2$ | 21.39 | | |
| $\tau_{00\ motusTagID}$ | 42.91 | | |
| $N_{\ motusTagID}$ | 63 | | |
| Observations | 126 | | |
| Marginal $R^2$ | 0.880 | | |

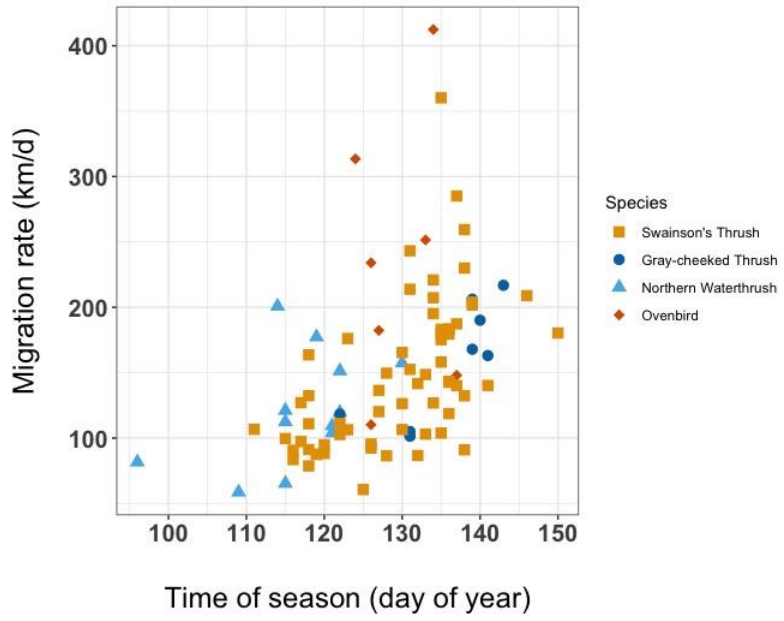


**Fig S4.** Relationship between average migration rate and day of year that birds were detected passing through the southern U.S. for the four species we tracked.

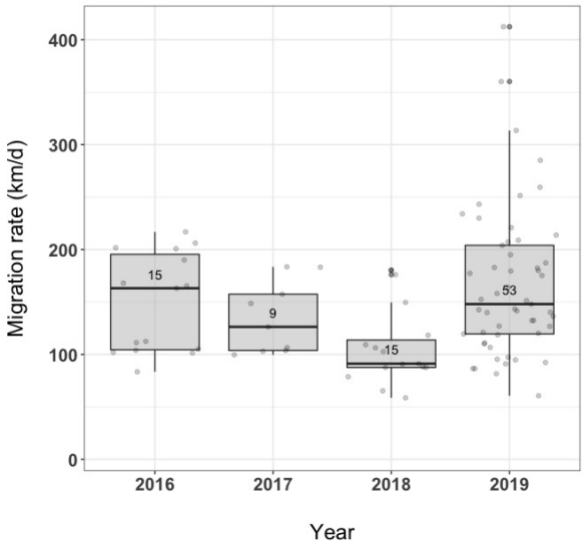


**Figure S5.** Interannual variation in migration rate. Numbers above boxplot medians show sample size each year.

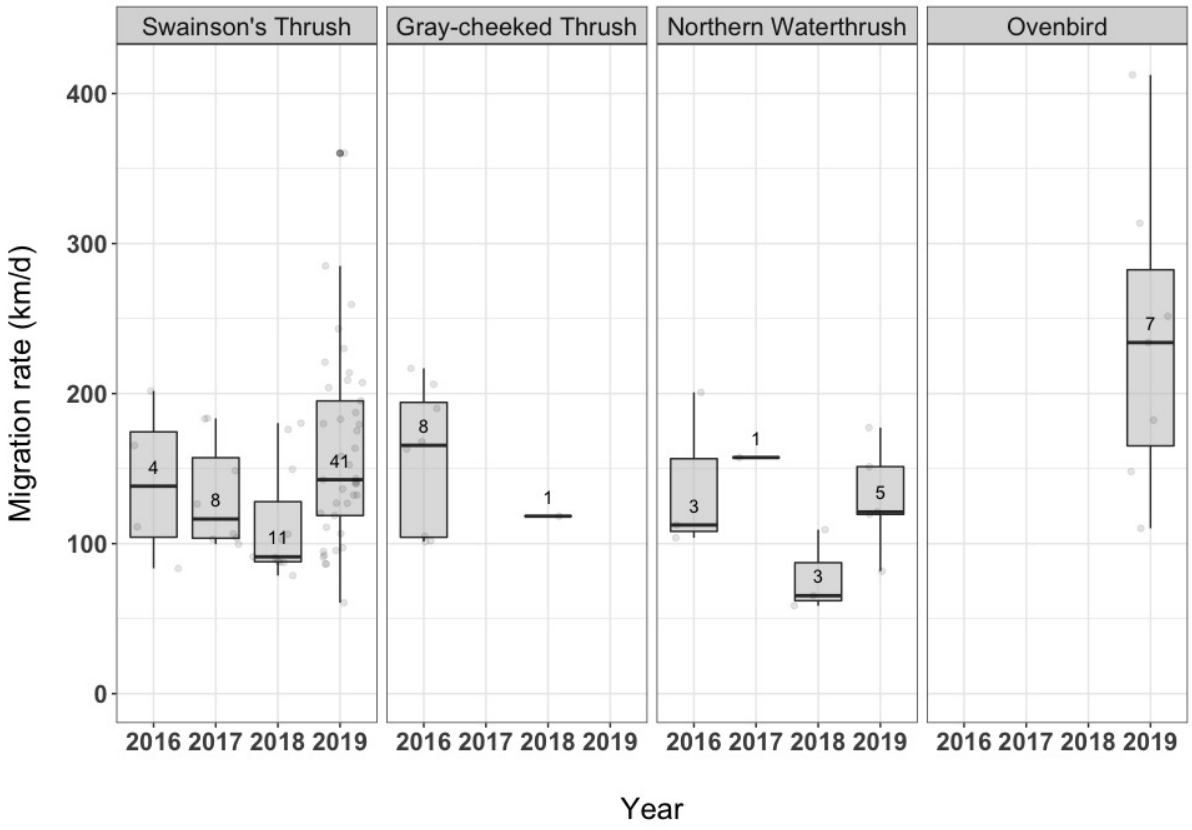


**Figure S6.** Interannual variation in migration rate by species. Numbers above boxplot medians show sample size each year.

**Supplemental Materials: Actual vs. Expected Spring Onset**

In addition to our primary questions, we were interested in determining if birds adjusted their migration timing based on actual phenological conditions they experienced (i.e., spring onset in the year they were tracked) or to the expected phenological conditions (long-term average spring onset). We tested the hypothesis that individual migration timing is more strongly related to actual phenology that birds experience *en route* instead of to the long-term expected spring phenology (Bauer et al. 2020). We predicted that migration day at both south and north bird detection locations would be positively related to both average spring onset day, indicating that migration timing has evolved to broadly coincide with the relatively predictable increase in

resource availability in spring, and to spring onset anomaly (number of days earlier or later than average that actual spring occurred), indicating that birds adjust their migration timing to annual phenological conditions they experience *en route*.

*Methods*

We used the National Phenology Network's product for spring onset day of year (**actual first leaf spring onset**) for each of the four years in which birds were tracked (2016 – 2019), as well as the 30-year Average Extended Spring Index First Leaf Date (annual leaf-out day averaged over years 1981 – 2010; **expected first leaf spring onset** day of year) and the First Leaf Anomaly for each year (difference between annual and average first leaf day) within a 10 km buffer of each bird detection. Estimation of **actual NDVI spring onset** and **expected NDVI spring onset** is described in Supplemental Materials - NDVI Spring Onset Analysis above.

We fitted separate linear regressions with migration day of year at either the south or north detection location as the response variable. For both models, we included as predictors average spring onset day, spring onset day anomaly (number of days earlier or later than average) in the year the bird was tracked, and species. The north migration day model also included distance (km) traveled between south and north detections as a control variable. To compare spring classification methods, we fitted both south and north models using NDVI and first leaf estimates of spring onset, resulting in four separate models.

*Results*

We obtained first leaf estimates for annual and average spring onset day of year at both southern and northern detection locations for 92 individuals. At southern sites, annual spring onset day estimated by first leaf ranged from 15 January to 3 February, with the same mean spring onset

day (25 January ± 5.02 days, n = 26 sites) as the 30-year average (25 January ± 1.91 days, range: 22 January - 29 January, n = 26). For the northern sites, which spanned a wider latitudinal range (42.9 to 51.8°N), mean annual first leaf spring onset day was 7 April ± 17.5 days (range: 21 February - 2 May, n = 70) and mean 30-year average first leaf spring onset day was 8 April ± 13.6 days (range: 8 March - 27 April, n = 70).

In the southern U.S., bird migration day of year was positively related to average first leaf spring onset day ($\chi^2$ = 4.38, p = 0.036, df = 1; Table S6). Contrary to our expectations, there was no relationship between migration timing and spring onset anomaly, reflecting annual conditions, in the southern U.S. (Table S6). For the model using NDVI spring onset estimates, neither average spring onset nor anomaly was related to bird migration timing in the southern U.S. (Table S7); species was the only important predictor of migration day. At the north site, neither first leaf average spring onset nor spring onset anomaly were related to bird migration day; only distance and species were important predictors of migration passage timing (Table S8). Similarly, neither average NDVI spring onset nor NDVI spring onset anomaly were related to bird migration day at the north site. As with the first leaf model, distance and species were the only important predictors of migration passage timing in the north (Table S9).

*Discussion*

Observed migration timing through the southern U.S. could reflect conditions during the stationary non-breeding period. For example, birds migrate later through the Gulf of Mexico Coast region in years when NDVI in their wintering ranges are low, reflecting drier winters (Paxton et al. 2014, Cohen et al. 2015). Phenology in passage areas south of the Gulf is a poor indicator of phenology within the U.S. (Cohen et al. 2015), meaning that birds may not obtain reliable information on annual variation in resource phenology until they arrive on the northern

Gulf Coast. Consequently, migration timing through this region may be more strongly correlated with average spring onset than with annual conditions, so that birds arrive at roughly appropriate times (Bauer et al. 2020).

**Supplemental Results: South migration day (first leaf spring onset)**

**Table S6.** Parameter estimates of the linear mixed-effects model for migration day at the southern detection location in relation to average spring onset and actual spring onset (anomaly), as estimated using first leaf spring index. The model included a random effect of year. Average first leaf spring onset day was positively related to bird migration day in the southern U.S., but actual spring onset day was not an important predictor.

| *Predictors* | *β (95% CI)* | *t* | *p* |
|---|---|---|---|
| Intercept | 94.65 (61.81, 127.49) | 5.73 | <0.001 |
| Average spring onset day (South) | 1.39 (0.07, 2.70) | 2.10 | 0.039 |
| Anomaly in spring onset day (South) | -0.41 (-0.97, 0.16) | -1.43 | 0.155 |
| Species: Northern Waterthrush | -11.92 (-16.90, -6.95) | -4.77 | <0.001 |
| Species: Gray-cheeked Thrush | 5.01 (-1.66, 11.68) | 1.49 | 0.139 |
| Species: Ovenbird | -2.59 (-9.14, 3.97) | -0.78 | 0.435 |
| **Random Effects** | | | |
| $\sigma^2$ | 59.77 | | |
| $\tau_{00\ year}$ | 5.81 | | |
| ICC | 0.09 | | |
| $N_{\ year}$ | 4 | | |
| Observations | 92 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.306 / 0.367 | | |

**Supplemental Results: South migration day (NDVI spring onset)**

**Table S7.** Parameter estimates of the linear model for migration day at the southern detection location in relation to average spring onset and actual spring onset (anomaly), as estimated using NDVI. Neither average nor spring onset anomaly predicted bird migration day; species was the only important predictor.

| *Predictors* | *β (95% CI)* | *t* | *p* |
|---|---|---|---|
| Intercept | 122.49<br>(88.19, 156.80) | 7.15 | <0.001 |
| Average NDVI spring onset day (South) | 0.11<br>(-0.35, 0.57) | 0.50 | 0.621 |
| Anomaly in NDVI spring onset day (South) | 0.21<br>(-0.15, 0.57) | 1.15 | 0.253 |
| Species: Northern Waterthrush | -17.33<br>(-24.60, -10.06) | -4.77 | <0.001 |
| Species: Gray-cheeked Thrush | 7.51<br>(-1.24, 16.27) | 1.72 | 0.091 |
| Species: Ovenbird | -1.52<br>(-9.27, 6.22) | -0.39 | 0.695 |
| Observations | 63 | | |
| $R^2$ / $R^2$ adjusted | 0.365 / 0.309 | | |

**Supplemental Results: North migration day (first leaf spring onset)**

**Table S8.** Parameter estimates of the linear model for migration day at the northern detection location in relation to average spring onset and actual spring onset (anomaly), as estimated from first leaf spring index. Neither actual nor expected spring onset day was an important predictor of bird migration day.

| *Predictors* | *β (95% CI)* | *t* | *p* |
|---|---|---|---|
| Intercept | 136.77<br>(126.84, 146.69) | 27.41 | <0.001 |

| | | | |
|---|---|---|---|
| Average spring onset day (North) | -0.03<br>(-0.18, 0.11) | -0.47 | 0.637 |
| Anomaly in spring onset day (North) | -0.04<br>(-0.23, 0.15) | -0.40 | 0.694 |
| Distance from South detection | 0.01<br>(0.00, 0.01) | 2.36 | 0.020 |
| Species: Northern Waterthrush | -9.59<br>(-13.75, -5.43) | -4.58 | <0.001 |
| Species: Gray-cheeked Thrush | 4.22<br>(-0.64, 9.08) | 1.73 | 0.088 |
| Species: Ovenbird | -4.15<br>(-9.35, 1.05) | -1.59 | 0.116 |
| Observations | 92 | | |
| $R^2$ / $R^2$ adjusted | 0.290 / 0.240 | | |

**Supplemental Results: North migration day (NDVI spring onset)**

**Table S9.** Parameter estimates of the linear model for migration day at the northern detection location in relation to average spring onset and actual spring onset (anomaly), as assessed from NDVI. As with the first leaf version of the model (Table S7), neither actual nor expected spring onset day was an important predictor of bird migration day.

| | **Bird passage day (North)** | | |
|---|---|---|---|
| *Predictors* | *β (95% CI)* | *t* | *p* |
| Intercept | 143.38<br>(118.41, 168.34) | 11.50 | <0.001 |
| Average spring onset day (North) | -0.08<br>(-0.32, 0.15) | -0.73 | 0.468 |
| Anomaly in spring onset day (North) | -0.31<br>(-0.74, 0.11) | -1.48 | 0.144 |
| Distance from South detection | 0.01<br>(0.00, 0.01) | 2.40 | 0.020 |

| | | | |
|---|---|---|---|
| Species: Northern Waterthrush | -7.51<br>(-14.01, -1.00) | -2.31 | 0.024 |
| Species: Gray-cheeked Thrush | 3.05<br>(-2.41, 8.52) | 1.12 | 0.267 |
| Species: Ovenbird | -6.32<br>(-11.27, -1.38) | -2.56 | 0.013 |
| Observations | 63 | | |
| $R^2$ / $R^2$ adjusted | 0.283 / 0.206 | | |

# Chapter 3: Close encounters: Behavioral responses of migrating songbirds to the perceived risk of predation

**Abstract**

Migrating birds face competing pressures to travel as quickly and efficiently as possible while minimizing the risk of predation *en route*. Migrating birds may encounter predators during stopover, when they land to rest and refuel, and can use a range of antipredator behaviors to reduce their immediate mortality risk, but doing so may impose indirect or delayed fitness costs that ultimately affect the success of migration. Despite their potential importance, antipredator behaviors in songbirds have been little studied relative to time and energy tradeoffs, even though humans have introduced invasive predators across the migration landscape. Antipredator behaviors depend on an individual's risk tolerance, which may be influenced by both intrinsic and extrinsic factors along with attributes of the predator (hunting style, native versus introduced). We tested the expectation that songbirds would respond with appropriate antipredator behaviors when confronted with predators during migratory stopovers, predicting that they would respond differently to a native aerial predator versus an introduced terrestrial predator.  captured migrating Gray Catbirds (*Dumetella carolinensis*) in spring and fall and exposed them to either a live domestic cat (*Felis catus*), a model hawk (*Accipiter* sp.), or a non-predator control stimulus. moved lower after exposure to a model hawk, as compared to the pre-exposure period, and resumed movement earlier after exposure to a live cat.  we used automated radio telemetry to measure the activity of migrants post-treatment. Post-release activity level did not differ between treatment and control groups, indicating that temporary predator exposure did not exert a persistent effect on migrants' activity levels. Birds on stopover appeared to respond to the domestic cat with appropriate antipredator behavior that may lower their immediate risk.

However, the influence of prolonged or repeated exposure to this introduced predator on the success of migration remains unclear and merits further investigation.

## Introduction

Nocturnal bird migration consists of alternating phases of flight and stopover, when birds land to rest and refuel. Conditions on stopover, and how birds respond to them, are key determinants of a successful migration (Moore 2018). Upon arrival at each successive stopover site, migrants must accurately assess and avoid potential threats while simultaneously under pressure to rapidly refuel to continue their journeys (Alerstam and Lindström 1990, Jenni and Schaub 2003b, Schmaljohann et al. 2022). Consequently, migrating birds balance the competing demands of minimizing time, energy expenditure, and predation risk; prioritizing one factor results in trade-offs with the others, because individuals cannot simultaneously travel with maximum speed, efficiency, *and* safety. Of these three optimization criteria, the effect of predation risk on migratory behavior has been studied extensively in certain shorebird systems (e.g., Ydenberg and Dill 1986, Lank et al. 2003, Pomeroy et al. 2006, 2008; Ydenberg 2022) but comparatively less in passerines and near-passerines (Alerstam and Lindström 1990, Alerstam 2011). However, predator avoidance is important throughout the life cycle (Barshep et al. 2011) and is likely a driving force behind the evolution of migration routes and timing in certain avian taxa (Alerstam 2011; Lank et al., 2003; Ydenberg et al., 2007).

While predators directly affect individual survival and prey population mortality rates via consumption, they also exert nonlethal or "non-consumptive" effects, influencing prey behavior or physiology (Lima 1998, Cresswell 2008b). Upon confrontation with a predator at stopover, a migrant may immediately respond with antipredator behaviors such as fleeing, reducing foraging activity, or increasing vigilance (Lima 1998, Schmaljohann and Dierschke 2005, Cresswell

2008b). For example, in response to a model hawk "flying" overhead during stopover, fat Gray Catbirds (*Dumetella carolinensis*) remained motionless while leaner migrants continued foraging, potentially reflecting the lean birds' high motivation to quickly refuel (Cimprich and Moore 2006; Moore 1994). Migrants may also display antipredator behaviors in the longer term, shifting into habitat patches that are perceived as less dangerous, departing from the site as soon as possible, or avoiding "risky" stopover sites altogether (Lindström 1990).

Antipredator behaviors can reduce predation risk, but this can come at a cost. Migrants carrying lower fat reserves are faster and more maneuverable when evading predators on stopover (Kullberg et al. 1996, 2000; Lind et al. 1999, Cimprich and Moore 2006), but carrying lower reserves may result in an overall slower migration speed if they have to stop to refuel more frequently (Alerstam and Lindström 1990, Schmaljohann et al. 2022). Migrants faced with predators at stopover sites may spend less time foraging, expend energy by flushing, or avoid feeding in otherwise resource-rich habitat (Ydenberg et al. 2007, Duijns et al. 2009, McCabe and Olsen 2015, Palmer et al. 2022). Such behaviors lower an individual's risk, or perception thereof, but may lead to lower fuel deposition rates or a longer stopover period, ultimately increasing the time required to migrate (Metcalfe and Furness 1984, Lindstrom 1990, Lima and Dill 1990, Lank and Ydenberg 2003, Schmaljohann and Dierschke 2005, Cresswell 2008b). Birds adopting a risk-averse, predation-minimizing strategy thus may improve their odds of *en route* survival but in doing so they may forego the opportunity to arrive at the destination as early as possible, which could reduce their reproductive prospects (Kokko 1999, Smith and Moore 2005a). Consequently, birds may be more tolerant of risk during non-breeding seasons (including migration) than during breeding, presumably because the need to quickly refuel during stopover overrides safety considerations (Mikula et al. 2018).

A number of studies confirm that avian predators, such as hawks and falcons, affect the behavior of migrating songbirds (Lind and Cresswell 2006b, Cresswell 2011, McCabe and Olsen 2015). In Europe, Bramblings (*Fringilla montefringilla*) on migration avoided attack by accipiters by moving into the denser cover of beech forests during mast years, even though foraging in the woods provides less energy than in open fields (Lindstrom 1990). On the U.S. Gulf Coast, two species of migrants moved into denser cover and reduced foraging activity in response to increased hawk activity (Cimprich et al. 2005b). If avoiding predators is not possible, birds may instead increase their refueling rates and attempt to depart a risky stopover site as quickly as possible, as observed in Blackcaps (*Sylvia atricapilla*) exposed to model hawks during fall migration (Fransson and Weber 1997a).

In addition to avian predators, migrating songbirds on stopover may also have to contend with terrestrial predators such as domestic cats (*Felis catus*), a widely introduced mammalian predator with which they have not co-evolved. While there has been little research during migration, free-roaming domestic cats are estimated to kill approximately 2.4 billion birds in the U.S. alone each year, representing the largest source of direct anthropogenic mortality for birds in the U.S. and Canada (Blancher, 2013; Calvert et al. 2013; Loss et al., 2013, 2015; Lowe et al., 2000). Domestic cats kill billions of birds annually elsewhere in the world (e.g., Woinarski et al. 2017, Li et al. 2021, Stobo-Wilson et al. 2022), representing an existential threat to wildlife globally (Nogales et al. 2013, Doherty et al. 2016a, Loss et al. 2022). During migration, over 20% of bird mortalities at Hongdo Island, a stopover site in South Korea, were attributed to free-roaming cats (Bing et al. 2012).

Free-roaming cats can kill birds on stopover but may also nonlethally influence migrating birds' behavior in ways that can scale up to affect fitness (Nemes et al. In Review). Nonlethal

effects of free-roaming cats remain understudied during all seasons (Medina et al. 2014, Loss and Marra 2017b). However, there is evidence for nonlethal effects of domestic cats on migratory birds during stationary periods of the annual cycle; the presence of cats reduces parental nest provisioning rates, increases nest predation by other species (Bonnington et al. 2013b, Greenwell et al. 2019), depresses activity levels (Fardell et al. 2023), increases flight initiation distance (Diaz et al. 2022), and causes overwintering birds to avoid or hesitate to approach food sources (Freeberg et al. 2016), Tryjanowski et al. 2015). However, information is lacking on the nonlethal effects of domestic cats on birds during migration, despite the potential for substantial impacts on bird behavior, habitat use, migration success, and ultimately population trajectories given the abundance and worldwide distribution of free-roaming cats. Furthermore, birds often use more human-altered habitat during migration than in other periods of the annual cycle (Seewagen and Slayton 2008, Matthews and Rodewald 2010, Seewagen et al. 2010, Zuckerberg et al. 2016), a pattern that may increase the probability of migrants encountering domestic cats, whose population densities are higher in anthropogenic landscapes (Lepczyk et al. 2004, Baker et al. 2005, Flockhart et al. 2016a).

In this study, we tested if migrating birds respond appropriately to the presence of domestic cats using an aviary experiment, and examined if the presence of this predator altered migratory behavior by tracking bird activity levels post-exposure. We confronted migrating birds with simulated predation threats (hawks and domestic cats) during stopover first to determine if they correctly perceive each predator as a threat and respond with antipredator behaviors, and then to determine if the type of antipredator response depends on the predator's hunting style (Caro 2005). We expected migrating catbirds would respond to hawks, which are aerial ambush predators, by moving low to the ground and decreasing activity to avoid detection (Cimprich and

Moore 2006). In contrast, we predicted that if migrating catbirds correctly perceived domestic cats as terrestrial ambush predators, they would move higher off the ground and increase their activity after exposure, indicating a desire to flee rather than freeze. To test for nonlethal effects of predator exposure on stopover behavior, we quantified the activity levels of Gray Catbirds post-exposure and compared them to control birds using automated radio telemetry. We predicted that birds would behave more cautiously after exposure to predators (Cimprich and Moore 2006), displaying a period of reduced activity relative to control birds.

## Methods

### Site and Study Species

We conducted experimental trials during spring and fall migration at Powdermill Avian Research Center (hereafter "PARC"), a bird observatory and banding station located within the Laurel Highlands region in Westmoreland County in southwestern Pennsylvania, U.S.A. (40°10'N, 79°16'W; Fig. S1). PARC conducts constant effort mist-netting year-round with nets open for 6h daily during spring and fall migration, starting 0.5h before sunrise (McDermott and DeGroote 2017). Habitat immediately surrounding the station consists of deciduous and mixed forest, a small field, and multiple ponds and streams. All birds captured are given a USGS band; age, fat score, morphometric measurements, and other standard data are collected by the bander in charge.

The study species, Gray Catbird, is a common and widely distributed Neotropical migratory songbird. This species breeds throughout much of the continental U.S. and southern Canada and overwinters in the southern U.S., Mexico, Central America, and the Caribbean (Ryder et al. 2011, Smith et al. 2020, Mancuso et al. 2021; Fig. S1). They are one of the most

common migrants at PARC during both spring and fall migration (between 400-500 new captures and 500-600 recaptures per year on average; A. Lindsay, personal communication). Gray Catbirds occur in human-altered landscapes throughout the annual cycle (Smith et al. 2020) and appear to be relatively common victims of cat predation in suburban areas (Balogh et al. 2011, Adalsteinsson et al. 2018). While the behavioral responses of Gray Catbirds to domestic cats specifically have not been described, they are known to respond to and occasionally confront other predators, including raptors (Burroughs 1923, Gottfried 1979, Smith et al. 2020, Redmond et al. 2020).

**Predator Exposure Experiment**

We designed an aviary experiment to assess the behavioral responses of Gray Catbirds confronted with predators during stopover. We constructed two free-standing aviaries, each measuring 1m x 1m x 1.5m, consisting of PVC pipe with bird netting stretched taut over the sides and ceiling (Heise and Moore 2003). The PVC frame was marked at equal intervals to facilitate height estimation with five classes in total (0 = ground level, 1 = bottom quarter, 2 = second quarter, 3 = third quarter, 4 = top quarter). We installed diagonally sloping perches made of natural tree branches, allowing birds to perch at any height, and draped each aviary with olive drab mosquito netting to provide an additional screen through which the bird's activities remained visible. Aviaries were separated by a free-standing wooden shed so that birds could not see one another, nor observe the other bird's experimental treatment or reaction (Fig. 1). This design allowed one individual to acclimate to its aviary while another bird was being tested. Following capture and banding, birds were released into the aviary and permitted to adjust to their surroundings for 30 minutes to 1 hour. During this time, an observer (CEN) monitored birds from within an observation blind located ~5m away for evidence of acclimation, including

preening and feeding. Birds were provided *ad libitum* food (live mealworms) and fresh water in dishes at ground level throughout the acclimation and trial periods.

Birds were assigned to one of three groups (Fig. 2): an "aviary control" group that was not exposed to a predator, an avian predator "hawk treatment" group exposed to a realistic model accipiter (Fig. 3a), or a mammalian predator "model cat treatment" group. In spring 2021, the cat treatment consistent of a realistic robotic cat and an additional "rabbit treatment" (realistic toy rabbit) group was included to serve as a non-threatening control to ensure that birds were responded to predators rather than to any novel object (Bonnington et al. 2013). However, birds showed little difference in response to the robotic cat versus the rabbit or control, indicating that the cat model was not sufficiently realistic to trigger an antipredator response and that the rabbit was unnecessary. Consequently, for trials in fall 2021, I trained a live pet cat to participate in the experiment (Fig. 3b). Fall 2021 birds were thus assigned at random to "hawk treatment," "real cat treatment," or "aviary control" groups. The model cat and rabbit treatment groups were discontinued and only control and hawk treatment observations from spring 2021 were retained for analysis.

Predator treatment stimuli were positioned outside of the aviary and covered with a camouflage cloth during the acclimation and pre-test periods. Each individual catbird was exposed to a single treatment. In spring 2021, we cycled through treatments sequentially (ex. rabbit, hawk, robot cat, control, repeat) to ensure an equal number of trials in each group and to ensure treatments were distributed evenly throughout the day and season. To account for any differences between aviary configuration that could influence behavior, we alternated trials between aviaries and presented all treatments sequentially in each aviary. In fall 2021, we followed this protocol for hawk and control trials, but only conducted trials with the pet cat 1 - 2

days per week to minimize transport stress. On those days, all birds received the real cat treatment. Cat days were spaced throughout the field season to control for time of season. The cat remained inside the blind with the observer during the acclimation period and was offered *ad libitum* food, water, treats, and litterbox access.

After the acclimation period, we began each trial by recording the individual's behavior for a 5-minute pre-test period, then presented the bird with the stimulus and recorded the same response variables for a 5-minute post-test period. The following response variables were recorded: (1) number of perch changes, (2) average height class within aviary, and (3) time (latency) to first movement. Height class was recorded at the start of the trial and at 30-second intervals thereafter, then averaged over the 5-minute period. Time to first movement (in seconds) was calculated as the time elapsed between the start of the post-test period and the bird's next perch change or hop (Cimprich and Moore 2006).

All treatments were presented or activated from within the observation blind (Fig. 2). The hawk model was attached via pulleys to a steel zipline stretched above the aviary and concealed during pre-test with a flap of lightweight cloth (Fig. 3a). The hawk was revealed by pulling a release pin via a string and allowing it to glide over the aviary, following Cimprich & Moore (2006) and Voelkl et al. (2016). For the real cat treatment, we released the pet cat (on a harness and leash) into a wire-sided dog crate at the start of the 5-minute post-test period; the observer remained next to the crate, concealed from view of the bird, to ensure that the cat remained calm while recording the bird's behavior (Fig. 3b). All birds were released immediately upon completion of the trial.

**Post-release Activity Level**

To investigate if predator exposure affects bird movement, we attached lightweight "nanotag" radio transmitters to a subset of Gray Catbirds prior to their inclusion in the aviary experiment. Tagged birds are detected by autonomous receivers in the Motus Wildlife Tracking System (Taylor et al. 2017), both locally and continentally (see Chapter 2 for additional details on the Motus network). PARC maintains several nearby Motus receivers, including one at the banding station. Catbirds that met minimum mass requirements were outfitted with Lotek nanotag transmitters – either model NTQB2-2 (~0.32g) or NTQB2-3-2 (~0.95g), depending on bird mass – using a leg-loop harness attachment (Rappole and Tipton 1991, Streby et al. 2015). Fat accumulation is a strong predictor of departure probability, so to control for differences in stopover duration based on fuel load, we primarily tagged birds classified as "lean" (fat score of 0 or 1). Tag deployments were spaced throughout each field season as evenly as possible, and tagged birds were assigned sequentially to each treatment group. We opportunistically tagged and immediately released additional birds to serve as a "tag control" group (i.e., individuals that were not held in the aviary).

To quantify activity levels, we downloaded tag detections from the motus.org database using the R package 'motus' (Birds Canada 2022) and filtered them using the default motusFilter setting to remove likely false detections (Crewe et al. 2018). We limited analysis to detections at the PARC banding station receiver (approximately 100m from the release site) that occurred within the first two hours after birds were released from the aviary (for individuals in the cat, hawk, or aviary control groups) or the first two hours after tagging (for individuals in the "tag control" group.) We calculated the coefficient of variation (CV) of each individual's tag signal strength (standard deviation in signal strength divided by absolute value of mean signal strength)

across the PARC banding station receiver's four antenna ports during the two-hour window. The CV serves as an approximation of the bird's activity level, with higher CV corresponding to more movement and lower CV corresponding to less movement (Deakin et al. 2021).

Capture, banding, nanotagging, and color marking of Gray Catbirds at PARC was conducted under the Carnegie Museum of Natural History's USGS Federal Bird Banding Laboratory permit number 08231 to Lucas DeGroote. The behavioral experiment was approved under UMCES Institutional Animal Care and Use Committee (IACUC) protocol S-AL-20-01.

**Classification of Migratory Status**

Gray Catbirds captured at PARC in spring and fall may be either individuals that breed locally or passage migrants (Smith et al. 2020). To separate out local breeders from migrants for analysis, we used a combination of banding records and nanotag detection patterns. Nanotagged individuals that were detected at Motus receivers north of PARC were considered passage migrants. Individuals that were recaptured at PARC during the summer months (July - August), recaptured between years, or that showed evidence of breeding (cloacal protuberance or brood patch) at the time of capture or recapture were considered local breeders. Nanotagged individuals detected at PARC Motus receivers during the summer months were likewise considered local breeders. All remaining individuals were classified as passage migrants. While it is possible that some locally breeding Gray Catbirds could have been incorrectly categorized as migrants if untagged, we believe these were reasonable criteria for distinguishing between groups.

## Analyses

### Predator Exposure Experiment

Despite sequentially assigning birds into treatment groups, the number of individuals in each group differed once local breeders were screened out. We used linear mixed-effects models (LMMs) or generalized linear mixed-effects models (GLMMs) with individual ID as a random effect to account for the pretest-posttest design, which is preferable to ANCOVAs when groups are unbalanced (O'Connell et al. 2017). LMMs were fitted using the R packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). Following the recommendations of (Zuur et al. 2009), we assessed model validity by inspecting residual plots for violations of homoskedasticity and other assumptions using R package performance (Lüdecke et al. 2021). We used the emmeans package (Lenth 2022) to conduct *post hoc* comparisons for pairwise differences between treatment groups and time periods (pre- or post-test), using the Kenward-Roger method for estimating degrees of freedom and a Bonferroni p-value adjustment for multiple comparisons (preferred to the Tukey adjustment when group sizes are unbalanced; Lee and Lee 2018)). With three comparisons, we considered contrasts to be statistically significant at an adjusted alpha level of 0.0167.

Average height within the aviary, a continuous response from 0 - 4, was modeled as the interaction between treatment ("hawk," "real cat," or "aviary control") and period ("pre-" or "post-" exposure to treatment) in an LMM with individual ID as a random intercept. The number of perch changes, a measure of activity level, was modeled using a negative binomial generalized linear mixed-effects model (GLMM) to accommodate overdispersion in the count response variable. However, variance of the random effect (individual ID was close to 0), causing model convergence issues and indicating that the random effect was not necessary. We re-fit the model

as a negative binomial generalized linear model in R package MASS (Venables and Ripley 2002). The time in seconds when the bird made its first perch change, with values between 0 and 300 (when the 5-minute period ended) was modeled using a negative binomial GLMM to accommodate overdispersion. Individual ID was included as a random intercept.

**Post-release Activity Levels**

To test for potential nonlethal behavioral effects of exposure to domestic cats, We assessed activity levels of tagged birds after release, measured as the coefficient of variation in signal strength, using linear regression with a fixed effect of treatment group. The model included time since sunrise (hours) as a continuous covariate to account for within-day variation in bird activity, which may be higher at dawn than midday (Robbins 1981).

**Figure 1**. Aviary field experiment setup. The observation blind (center) is positioned equidistant from the two aviaries and in line with a wooden shed, which separates the aviaries from view of one another and provides an attachment point for the hawk ziplines.

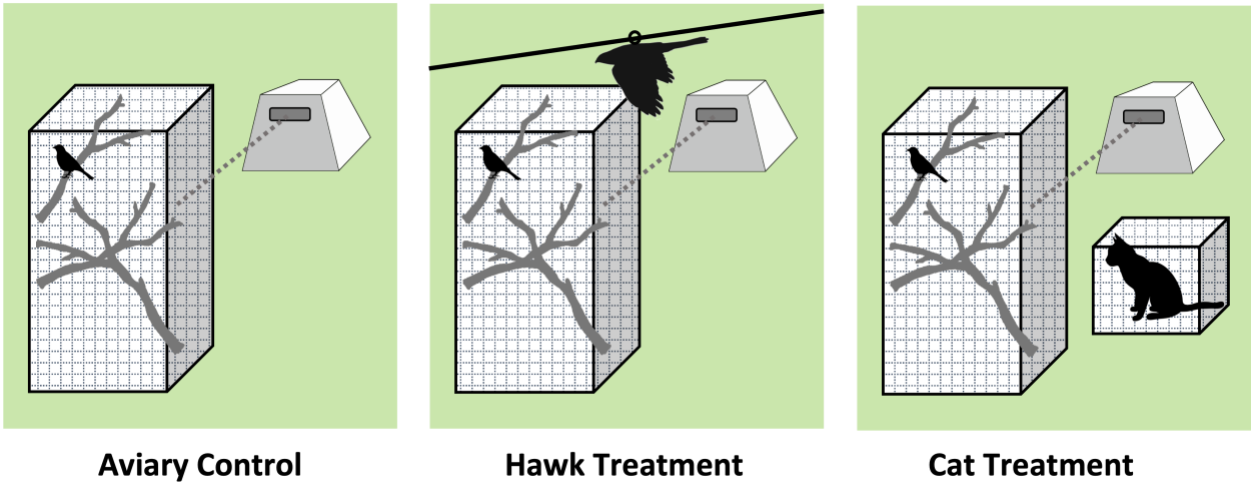


**Fig. 2.** Design of aviary experiment. Each bird was released into an aviary with natural perches of various heights and its pretest and posttest behaviors were recorded by an observer concealed within a nearby observation blind. Dotted line indicates line of sight from blind approximately 5m away from the aviary.


**Figure 3** (a). Model hawk on zipline as seen from the perspective of a bird in the aviary. (b) Modification to observation blind allowing pet cat to be released into crate and viewed by the catbird subject for the 5-minute post-test period.

## Results

During spring (27 April - 21 May) and fall (4 September - 11 October) 2021, we tested 103* Gray Catbirds in aviary trials at PARC. Fourteen trials were omitted due to incomplete data (ex. birds escaped or were released during inclement weather prior to completion of the full trial) or other environmental disturbances that may have confounded behavior (ex. high winds, nearby lawnmowers, enthusiastic construction workers). Of the remaining 89 individuals that were tested in the aviary, 18 were deemed local breeders (or indeterminate migratory status) and were excluded from further analysis, leaving n = 71 migrants. Of these, 60 individuals were aged as hatch year or second year (HY/SY for fall and spring captures, respectively), and 11 as after hatch year or after second year (AHY/ASY). In total, I conducted experimental trials with 11 migrants in the spring and 60 in the fall. (*Trials with the model cat (n=14) and model rabbit (n = 12) were excluded from analysis and not included in these totals).

**Table 1.** Sample sizes per treatment group for the predator exposure experiment at PARC. Migratory status ("migrants" versus "local breeders") was assessed with banding, physiological, and tracking data. "Unknown" birds were those for which migratory status could not be ascertained with confidence.

| **Treatment Group** | **Migrants** | **Local breeders / Unknown** | **Total Tested** |
|---|---|---|---|
| Control (aviary) | 26 | 10 | 36 |
| Real cat | 20 | 1 | 21 |
| Hawk | 25 | 7 | 32 |
| | **71** | 18 | 89 |

Sixty-four Gray Catbirds were nanotagged to examine their activity levels. Two tags were never detected for undetermined reasons. Nine individuals were released immediately to serve as "tag

controls" for comparing activity levels and were not tested in aviary trials. Of the remaining tagged birds, 14 were assigned to the aviary control group, 15 to the hawk treatment group, and 7 to the real cat treatment group.

**Predator Exposure Experiment**

Average bird height within the aviary (Figure 4) differed by treatment group and time period (treatment x period interaction: $F(2,68) = 4.016$, $p = 0.022$). Across all groups, average height was greater in the pre-test (mean = $3.33 \pm 0.9$ SD) than the post-test ($3.12 \pm 1.0$). During the post-test period, birds in the hawk group moved significantly lower than during the pre-test (simple contrasts for period: $\beta = 0.527$, SE = 0.168, df = 68, t-ratio = 3.068, $p = 0.003$), but birds in the control and cat groups did not show meaningful differences between pre- and post-test height. Pre-test height differences approached statistical significance at the adjusted $\alpha = 0.0167$ between birds in the hawk and cat groups ($p = 0.017$) and between birds in the hawk and control groups ($p = 0.027$). Height differences during the post-test for birds in the hawk group were significantly lower than those in the control group ($\beta = 1.3111$, SE = 0.239, df = 109, t- ratio = 5.494, $p < 0.0001$) and the cat group ($\beta = -0.973$, SE = 0.256, df = 109, t-ratio = -3.808, $p < 0.001$). Birds in the control and cat groups did not differ in post-test height. The model provided good overall explanatory power for height (conditional $R^2 = 0.61$, marginal $R^2 = 0.24$).

Across all groups, the average number of perch changes was lower in the pre-test period ($27.2 \pm 34$) than during the post-test period ($32.5 \pm 30$). The number of perch changes (Figure 5) did not differ meaningfully from pre- to post-test periods in any of the treatment groups, nor between treatment groups (likelihood ratio $\chi^2$ for treatment x period interaction = 0.116, df = 2, $p = 0.944$); the model for perch changes had poor explanatory power overall (Nagelkerke $R^2 = 0.021$).

The average time of first movement (in seconds) was later in the pre-test period across all groups (163.0 ± 137) as compared to the post-test period (106.0 ± 122). Birds in all three groups began moving earlier (Figure 6) during the post-test period than in the pre-test period (period: $\chi^2$ = 9.515, df = 1, p = 0.002), but the treatment group x period interaction was not an important predictor of first movement time (treatment x period interaction: $\chi^2$ = 1.899, df = 2, p = 0.387). Pairwise comparisons indicated that birds in the cat treatment group moved significantly earlier at the adjusted significance level of $\alpha$ = 0.0167 during the post-test (simple contrasts for period: ratio = 2.61, SE = 0.909, z-ratio = 2.756, p = 0.006), but neither control nor hawk group birds showed a difference between pre- and post-test movement times. The model explained a good proportion of the variance in first movement time overall (conditional $R^2$= 0.51, marginal $R^2$ = 0.11).

**Post-release Activity Levels**

After release, tagged birds exhibited similar activity levels as measured by CV of signal strength (Figure 7), regardless of treatment group (treatment: F(3,39) = 1.561, p = 0.214). Activity level also did not vary by time of day (hours after sunrise: F(1,39) = 2.35, p = 0.133), nor by migratory status (F(1,39) =1.682, p = 0.202). Overall, the model only explained a small proportion of the variance ($R^2$ = 0.148, adjusted $R^2$ = 0.039, F(5, 39) = 1.359, p = 0.261).

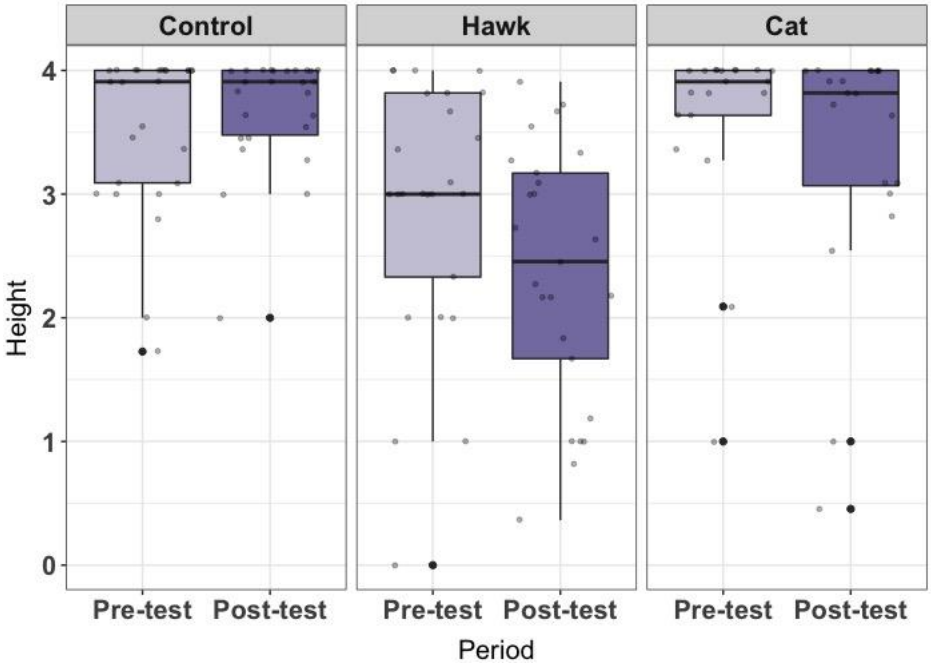


**Figure 4.** Average height within aviary during pre-test and post-test periods. Individuals in the hawk treatment group moved lower in the aviary following exposure to the predator ($p = 0.003$).

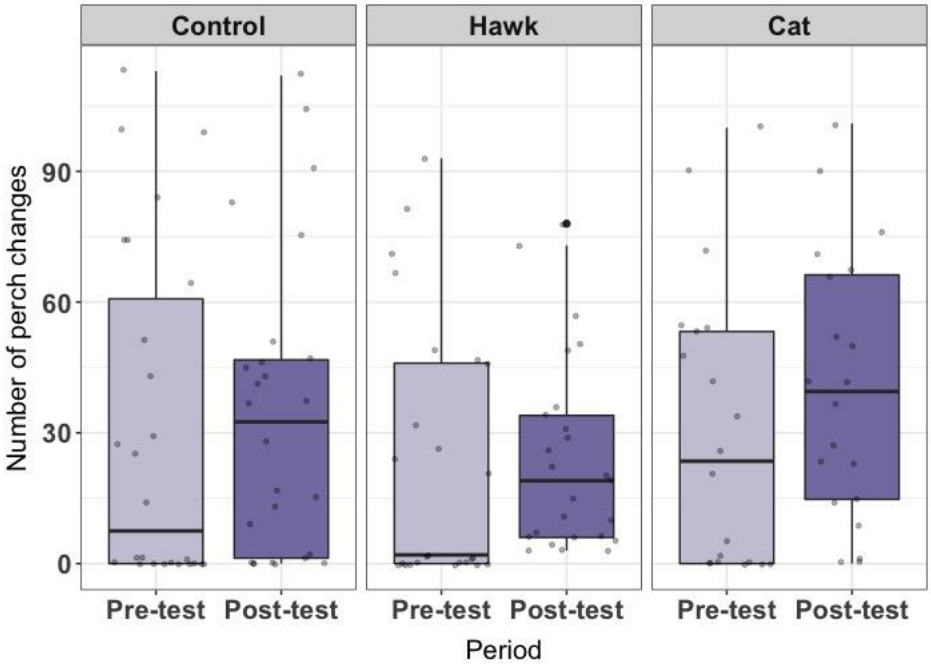


**Figure 5.** Number of perch changes during pre-test and post-test periods for each treatment group. The number of perch changes did not differ between periods within any group, nor did it differ between treatment groups.

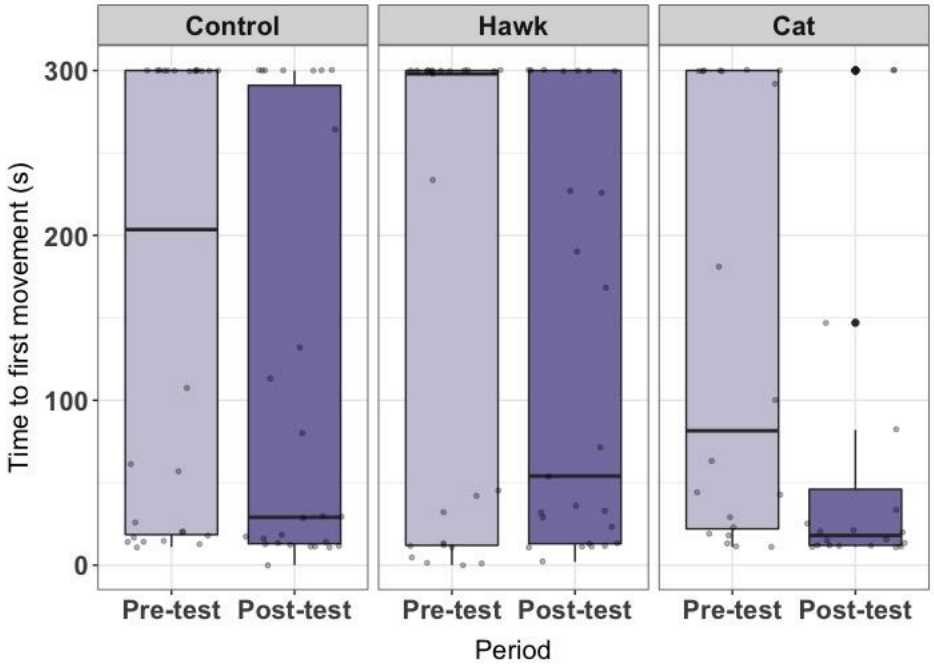


**Figure 6.** Timing of first movement (in seconds) during the 5-minute pre-test and 5-minute post-test periods. Individuals in all groups moved earlier during the post-test period than during the pre-test, but the difference was only important for the cat treatment group (p = 0.006).

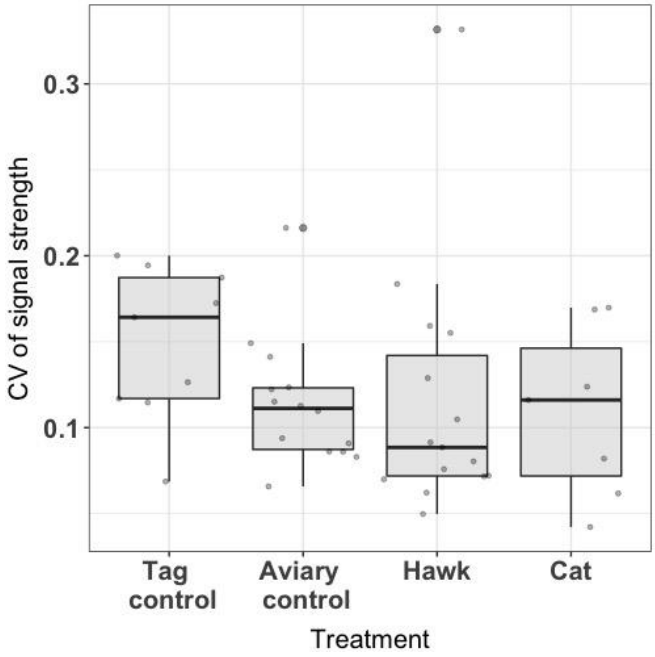


**Figure 7.** Coefficient of variation (CV) of signal strength in detections of nanotagged birds during the first two hours post-release. Birds in the "tag control" group were released immediately after nanotagging, while birds in the "aviary control" group were released into the aviary after tagging but were not exposed to a predator treatment. CV of signal strength did not differ by treatment group (p = 0.214).

## Discussion

Nonlethal effects of predators influence bird foraging behavior, habitat selection, and other individual-, population-, and community-level dynamics during all phases of the annual cycle, including migration (Lima 1998, Preisser et al. 2005, Cresswell 2008). In this regard, predators exert nonlethal effects by influencing prey behavior that may even outweigh the costs of direct predation (Lima 1998, Preisser et al. 2005, Cresswell 2008b). Birds that correctly perceive predators as a threat may display antipredator behaviors that successfully lower their risk, but which come at the expense of minimizing time or energy expenditures on migration (Alerstam and Lindström 1990, Lindstrom 1990). Alternatively, if birds don't perceive predators as a threat, or respond with behaviors that are not appropriate to the type of predator, they may incur higher risk of mortality (Cresswell 2008b). Consistent with predictions, we found that migrating Gray Catbirds appeared to perceive both hawks and domestic cats as threats, changing their behavior in the short-term. Overall, behaviors were reasonably well-matched to the predator: birds moved lower in the aviary in response to the aerial hawk and resumed movement sooner (i.e., did not freeze) in response to the terrestrial cat. Freezing or otherwise reducing movement to escape detection is probably an advantageous response in non-flocking songbirds whose avian predators are capable of highly maneuverable flight (Cimprich et al. 2005b, Cimprich and Moore 2006); in contrast, taking wing may be a better response to a flightless predator like a domestic cat, or in cases where concealment is not possible (e.g., Kullberg et al. 1996, 2000; Lind et al. 1999).

Although we expected Gray Catbirds to freeze after exposure to the model hawk, individuals in this study did not show a statistically significant difference in how quickly they

moved after exposure to the hawk model versus before. Similarly, we expected birds to move less after exposure to the hawk and more after exposure to the cat, yet we did not observe any effect of treatment group on the perch change activity metric. There was substantial variation in both pre- and post-test scores for all response variables, though pre-test scores did not differ significantly between groups. Consistent with this variability, we observed a spectrum of baseline activity levels and apparent personalities in Gray Catbird subjects (Nilsson et al. 2014); for example, some individuals acclimated quickly to the aviary, while others continued vigorous escape attempts for much longer. We did not have facilities in which to house Gray Catbirds for an extended period; it is possible that allowing birds to adjust to captivity for longer before starting the experiment would have allowed us to better distinguish noise from signal (Moore and Simm 1986, Moore 1994, Lind et al. 1999).

Other elements of our experimental design, along with both intrinsic and extrinsic factors (Jenni and Schaub 2003b, Moore 2018, Schmaljohann et al. 2022), may have influenced Gray Catbird behavior in ways we did not account for. How an individual bird behaves when faced with a predator depends on a combination of factors including fat reserves and time of season, both of which can influence motivation to refuel quickly and prioritize speed over safety (Cohen et al., 2012; Dierschke 2003; Jenni & Schaub, 2003; McCabe and Olsen, 2015; Smith & Moore, 2005). The experimental design attempted to control for factors that might influence bird behavior, including time of day, time of season, and fat score, through sequential assignment of birds into treatment groups. Behavior may differ between spring and fall migration (Seewagen et al. 2013); birds are typically considered to be under greater time pressure and migrate faster in the spring, which could manifest in greater risk-taking behavior in comparison with birds exposed to predators during the more protracted fall migration (Fransson and Weber 1997b,

Nilsson et al. 2013, Bennett et al. 2019). While we initially intended to test for differences in behavior between spring and fall migrants, our sample sizes were too small to incorporate a seasonal effect. Similarly, older birds with more experience may exhibit different foraging behaviors on stopover 4/18/2023 8:37:00 AM as well as different risk tolerance and antipredator behaviors (Hope et al. 2014), but we did not capture enough individuals across age classes to evaluate this effect. Neither could we test for differences in behavior by sex (Deakin et al. 2019) due to the lack of sexual dimorphism in this species. Although we evaluated catbirds for migratory status (passage migrants versus local breeders) and excluded both confirmed breeders and individuals for which we were uncertain, it is possible that the sample may have included some individuals that were not passage migrants. Prey species are expected to display some degree of antipredator behavior throughout the annual cycle, but risk tolerance is higher during migration than breeding (Moore and Simm 1986, Moore 1994, Mikula et al. 2018), and accidental inclusion of local breeders may have reduced our ability to distinguish behavioral differences.

We had predicted that nanotagged birds exposed to predators would show a reduction in activity level after release from the aviary, reflecting increased caution. However, we did not observe any differences between controls and treatment groups during the two-hour automated telemetry monitoring period. This apparent lack of response has several possible non-exclusive explanations. If any dampening of foraging behavior occurred, it may have been short-lived and too transient to detect over this time window. Importantly, the majority of birds we tagged had little to no fat reserves, and would have had a strong motivation to quickly resume fueling regardless of predation risk (Dierschke 2003b, Cimprich and Moore 2006). Migrating raptors sometimes reach high densities at migratory hotspots and bottlenecks, where they can exert

considerable predation pressure and fear effects on songbird prey (Lindström 1989b, Cimprich et al. 2005b, Cohen and Satterfield 2020, Samraoui et al. 2022), yet songbirds must forage nonetheless, if only to acquire enough fuel so that they can leave and find a safer stopover site. Consequently, unless predation risk is exceptionally high or continuous, a brief and temporary decrease in foraging behavior should be preferable to a sustained reduction in activity, which would negatively affect refueling rate and perhaps migration speed.

The fact that Gray Catbirds on stopover responded to domestic cats in the short-term indicates that catbirds are not completely naïve to the threat of this introduced predator. The lack of activity changes post-release may also suggest that their antipredator responses do not persist long enough to negatively affect activity and ultimately refueling rates on stopover. On the other hand, our experiment involved exposing birds to a captive cat that could not stalk or pounce upon them for a very short period (5 minutes). Thus, birds may have assessed the situation as less threatening than actual encounters with cats on stopover. If birds in the wild perceive cats to be more acutely or persistently threatening, they may exhibit stronger antipredator behaviors that induce chronic stress or necessitate greater trade-offs with foraging and fuel deposition (Cresswell 2008b).

This study provides evidence that migrating songbirds do appear to perceive domestic cats as a threat and respond by changing their behavior. To what extent the catbirds' antipredator responses successfully reduce cat predation mortality remains an open question. Similarly, any negative consequences of antipredator behavior on migration success remain unclear. Illustrating the complexity of translating observed behavior into inference about fitness effects, migrating birds frequently use multiple strategies to alleviate predation risk. Thus, a behavior that researchers interpret as "risky" may actually be offset by other antipredator behavior(s) through

"predation risk compensation" (Lind and Cresswell 2006b). Despite this, evidence is mounting that exposure to anthropogenic stressors on migration, including free-roaming cats, can produce nonlethal effects that ultimately influence fitness (reviwed by Nemes et al. In Review). Because of the wide distribution and high abundance of cats throughout migration corridors, birds may encounter these introduced predators at multiple points within their journeys, and could experience cumulative or interacting effects (e.g., Doherty et al. 2015, Rebolo-Ifrán et al. 2021) that ultimately reduce migration success. As a domesticated species, cats are not native to any ecosystem and occur in much higher densities than native raptors in many regions (Rodewald et al. 2011, Loss and Marra 2017b, Loss et al. 2022), which may magnify their impacts on bird behavior through repeated or cumulative fear effects. Consequently, any nonlethal behavioral or physiological changes that cats induce, however small, represent an additional challenge for migrating birds in an already perilous journey (Vickery et al. 2014, Bairlein 2016, Dutta 2017, Rosenberg et al. 2019, Wilson et al. 2020, Yong et al. 2021, Richard et al. 2021, Buchan et al. 2022).

**Acknowledgments**

We are grateful to the many staff and volunteers at PARC who supported this project. Annie Lindsay, Mary Shidel, and Luke DeGroote helped coordinate logistics and provided invaluable assistance in the field. Mary Shidel graciously shared PARC's catbird banding data. John Piasecki at UMCES assisted with construction and assembly of the aviaries. Bobby Ankney and Ryan Carter at PARC and Larry and Ellen Moon of Golden Moon Labradors shared tools, equipment, and construction expertise. Sarah Hamer at Texas A&M University and Peter Marra at Georgetown University provided funding for nanotags. John Hoogland (UMCES) and Frank Moore (University of Southern Mississippi, emeritus) offered useful insights on designing and

refining the behavioral experiment. The UMCES Appalachian Laboratory administrative staff and UMCES IACUC members provided additional logistical support. Joely DeSimone graciously provided feedback on the draft of this chapter. Finally, this research project would not have been possible without the cooperation and support of Veery, the world's best cat.

# Chapter 4: Density of free-roaming domestic cats in San Juan, Puerto Rico: Potential impacts on birds and other wildlife


## Abstract

Free-roaming domestic cats (*Felis catus*) have contributed to the extinctions of many species and island wildlife are especially vulnerable. Caribbean islands host a high diversity of both resident endemic bird species and seasonal migrants, for which threats in the non-breeding range are often overlooked. However, domestic cat impacts remain understudied in tropical regions, due in part to challenges in accurately estimating abundance and predation. We designed a camera trapping study to rigorously estimate cat densities across a gradient of urbanization in San Juan, Puerto Rico, predicting that densities would be positively related to urbanization due to cats' reliance on human subsidies. We deployed arrays of camera traps at 16 sites across an urban gradient during the temperate winter in 2019 and identified individual cats captured on the cameras from their unique markings. We estimated cat densities and movement parameters at urban, suburban, and exurban sites using spatial capture-recapture models based on over 30,000 photos of cats, including 524 uniquely identifiable individuals. Model-estimated densities across the municipality supported the prediction of higher densities in urban areas as compared to suburban and exurban areas, ranging from 48 ± 8 (SE) cats/km$^2$ in exurban areas to 473 ± 40 cats/km$^2$ in urban areas. While Neotropical cities and suburbs can provide habitat for resident and migratory bird species, high densities of this introduced predator suggest that domestic cats may pose a substantial threat to native wildlife.


## Introduction

Free-roaming domestic cats (*Felis catus*) pose a major threat to birds and other wildlife taxa worldwide (Blancher 2013a, Calvert et al. 2013b, Loss et al. 2013b, Woinarski et al. 2017,

Seymour et al. 2020, Li et al. 2021, Sedano-Cruz 2022). Island fauna and endemic species are particularly vulnerable to domestic cat predation due to their small population sizes and naïveté to introduced predators (Courchamp et al. 2003, Bonnaud et al. 2011, Medina et al. 2011, Nogales et al. 2013). Domestic cats have caused or contributed to the extinctions of at least 63 species of birds, mammals, and reptiles (Doherty et al. 2016b), 33 of which have occurred on islands (Medina et al. 2011), and they currently threaten hundreds of other imperiled species (Sedano-Cruz 2022). In addition to direct predation, the presence of free-roaming cats can negatively influence wildlife behavior, health, habitat use, and ecological interactions (Crooks and Soulé 1999, Bonnington et al. 2013, Medina et al. 2014, Loss and Marra 2017, Kays et al. 2020, Loss et al. 2022, Fardell et al. 2023; see also Chapters 1 and 3). Furthermore, free-roaming cats are a public health concern because they transmit diseases to humans and to other domestic animals (Gerhold and Jessup 2013, Chalkowski et al. 2019, Aguirre et al. 2019), and may be regarded as a nuisance due to fighting, urination and defecation, and attraction of pest species to feeding stations (Ash and Adams 2003, Gunther et al. 2015). The variety and ubiquity of these impacts have prompted the International Union for the Conservation of Nature to list the domestic cat as one of the world's 100 worst introduced species (Lowe et al. 2000). Therefore, there is an immediate and ongoing need for research and science-based management strategies that protect insular wildlife from free-roaming cats (Bonnaud et al. 2011, Medina et al. 2014, Doherty et al. 2016b, Lepczyk et al. 2022).

Caribbean islands exhibit a high degree of biodiversity and endemism; the unique species and ecosystems of this region face pressure from human alterations that include introduced mammalian predators (Wunderle, Jr. 2008). The island of Puerto Rico in the Greater Antilles is home to a diverse avifauna that includes 17 endemic species, several of which are classified as

endangered, threatened, or vulnerable (Miller and Lugo 2009, Nytch et al. 2015, Castro-Prieto et al. 2021). During the temperate winter, Puerto Rico's year-round resident bird community is supplemented by an influx of Nearctic-Neotropical migrants, including several species of conservation concern (García et al. 2005; Wunderle & Waide 1993; Wunderle & Waide 1994). In total, over half of the bird species documented in Puerto Rico are regular migrants or vagrants (Anadón-Irizarry et al. 2009). Although Nearctic-Neotropical migrant birds often spend the largest percentage of the annual cycle in stationary non-breeding areas (Marra et al. 2015), we know little about cat predation or nonlethal effects of cats on birds during this period. To compensate for high mortality during migration, long-distance migrants are assumed to depend on a life history strategy of high adult survivorship during the stationary periods (Sillett and Holmes 2002b, Rockwell et al. 2017b, Paxton and Moore 2017, Rushing et al. 2017, Dokter et al. 2018), meaning that population stability and persistence of migratory species may be especially sensitive to changes in non-breeding season survival (Calvert et al. 2009, Dokter et al. 2018). Although the effects of free-roaming cats and other introduced mammals on migratory and resident birds in the Caribbean have received limited study (Nytch et al. 2015, Mohammed et al. 2022), cats are well established in Puerto Rico and may threaten the island's wildlife (Miller and Lugo 2009, Rodríguez-Durán et al. 2010, Castro-Prieto and Andrade-Núñez 2018, Zimmerman et al. 2021), including endemic and endangered species such as the Yellow-shouldered Blackbird *Agelaius xanthomus* (López-Ortiz et al. 2002) and the Puerto Rican Parrot *Amazona vittata* (Engeman et al. 2006).

A primary challenge to understanding the impacts of free-roaming cats on wildlife in Puerto Rico and elsewhere in the Caribbean is a lack of information on cat abundance and distribution. While free-roaming cat abundance or density has been rigorously estimated in

several locations (Sims et al. 2008, Flockhart et al. 2016, Legge et al. 2017, Dias et al. 2017, Cove et al. 2018, 2023; McDonald and Skillings 2021; see also Nogales et al. (2004) for a review of cat densities on islands), estimates remain sparse for the Caribbean and the Neotropics in general. Geographic variation in climate, habitat, and ecological interactions, along with differences in human attitudes and behavior that include food provisioning, cat sterilization rates, and pet ownership, can all influence free-roaming cat activity and population dynamics (Finkler et al. 2011, Newsome et al. 2015, Flockhart and Coe 2018, Maeda et al. 2019, Bischof et al. 2022). Although there is a substantial body of research on the multifaceted ecological impacts of free-roaming cats, much of this research has been conducted in a limited number of geographic regions and countries (Loss et al. 2022, Orduña-Villaseñor et al. 2023). The U.S. Forest Service, which conducts extensive research and management in Puerto Rico, is especially concerned with invasive species removal and lists one of its top priorities as "Develop[ing] spatial maps of occurrence of individual invasive species and concentrations of species and overlay[ing] these with maps of native animal species concentrations to determine priority locations for focusing eradication efforts" (Finch et al. 2010).

Estimating cat density and spatial distribution is therefore a necessary step in determining their effects on wildlife, prioritizing areas for population management, and assessing if management actions are effective to reach conservation goals. Domestic cats are frequently associated with humans and tend to occur at their highest densities in human-dominated landscapes (Mirmovitch 1995, Bateman and Fleming 2012, Bennett et al. 2021), though they persist at low densities even in protected areas (Dayer et al. 2020) and remote regions without human subsidies (Legge et al. 2017). Despite the potential hazards from introduced predators (Mella-Méndez et al. 2019, 2022), urban and suburban areas in the Neotropics provide habitat

for many species of migratory and resident birds and other wildlife (Ortega-Álvarez and MacGregor-Fors 2009, MacGregor-Fors et al. 2010, Puga-Caballero et al. 2014, MacGregor-Fors et al. 2016, Escobar-Ibáñez et al. 2020, Pacheco-Muñoz et al. 2022a). Although spatial overlap between cats and birds does not necessarily confer information about the magnitude of the threat (Tulloch et al. 2015), it is a prerequisite for potentially harmful effects of free-roaming cats on wildlife (Herrera et al. 2022).

To address these knowledge gaps, we conducted a camera trapping project to estimate the density and spatial distribution of free-roaming cats along an urban gradient in the municipality of San Juan, Puerto Rico, the island's most populous region. We used a spatial capture-recapture approach (Efford et al. 2009) model density and space use of cats while accounting for differences between urbanization levels. We predicted that cat densities would positively reflect human population density and thus would be highest at sites classified as "urban", intermediate at "suburban" sites, and lowest at "exurban" sites.

## Methods

### Study Area and Camera Trapping

Between 2 January - 14 February 2019, we deployed trail camera arrays across the San Juan Metropolitan Area of northeast Puerto Rico, the island's most populous region (Fig. 1). Sites were broadly classified into three land use categories *a priori* on the basis of percent impervious surface derived from the Landsat Global Man-made Impervious Surface dataset (Brown de Colstoun et al. 2017). Categories were exurban (0 – 25% impervious surface), suburban (25.001 – 67%), and urban (67.001 – 100%). Sixteen study sites (5 urban, 5 suburban, 6 exurban), consisting of 8 - 10 camera traps each, were established within the municipality of San Juan, one of six municipalities that comprise the San Juan Metropolitan Area (Fig 1). Cameras were

spaced approximately 100 m apart and baited every other day with dry cat food during the trapping period. To maximize spatial coverage, we deployed cameras in four successive time blocks during January and February 2019, during which cameras were distributed across four sites and allowed to collect data for six days before being rotated to new sites. We sorted and classified all photos to species and individual in Adobe Lightroom using exif metadata tags, then used package camtrapR (Niedballa et al. 2016) to extract tag data and generate individual record tables and spatial detection histories. Individuals that could not be identified were excluded from the analysis, as were all juveniles. When possible, we classified individuals as male (based on observed genitalia or clear secondary sexual characteristics; Natoli 1985) or female (based on genitalia or calico/tortoiseshell fur patterns, which are rarely found in male cats; Bamber and Herdman 1927). All cat identifications were made by a single observer (C. Nemes) for consistency. All analyses were conducted in Program R (R Core Team 2020).

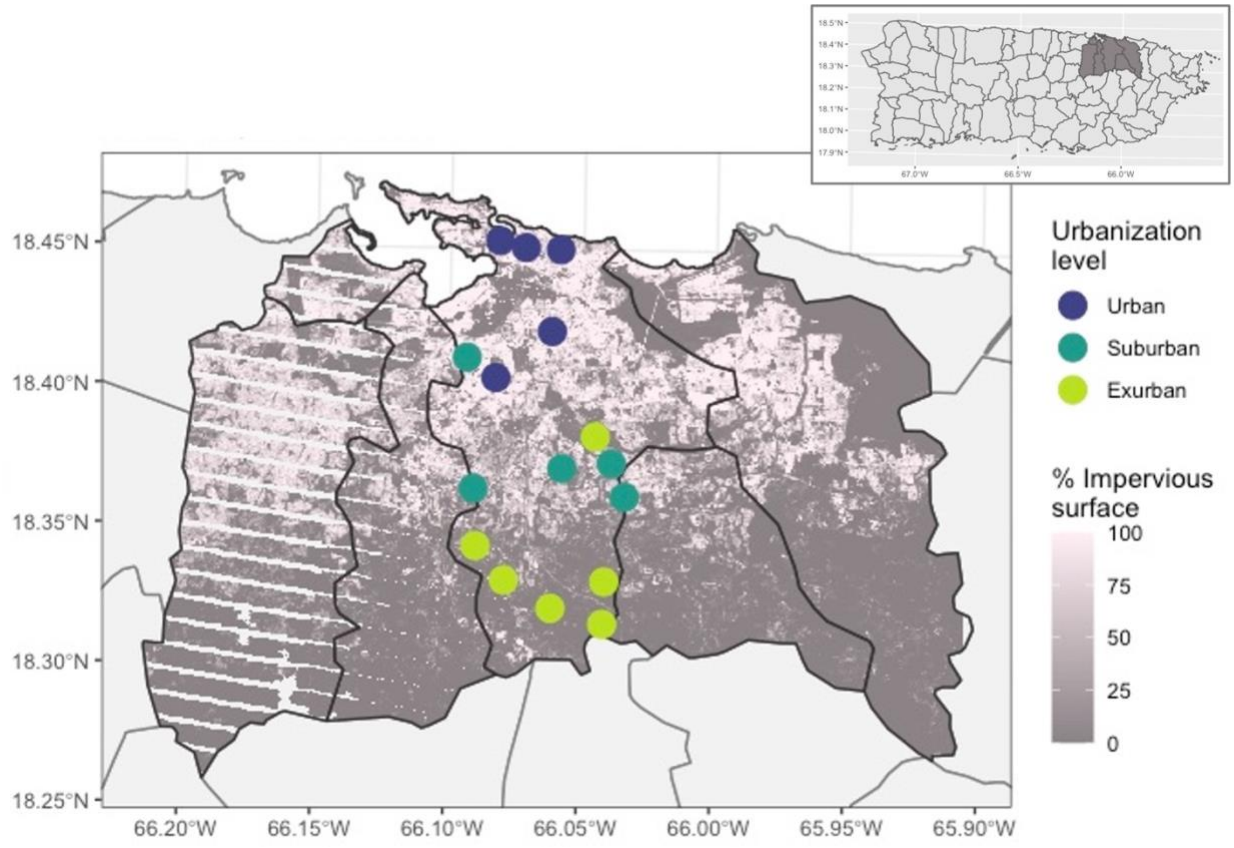


**Fig. 1.** Locations of camera trapping arrays and their urbanization designation based on percent impervious surface within the San Juan Metropolitan Area on the island of Puerto Rico (inset map).

## Analyses

### Spatial Capture-Recapture Model

Domestic cats, like many wild felid species, have unique coat patterns that allow individual recognition without the need for researchers to physically capture and mark animals (Mirmovitch 1995, Elizondo and Loss 2016). When some or all members in a population are uniquely identifiable, spatial capture-recapture (SCR) models allow direct estimation of animal density based on individual spatial encounter histories at known detector locations, such as camera traps

(Royle et al. 2013). We analyzed camera trapping data in a likelihood-based framework (Borchers and Efford 2008) using a multi-session, sex-structured SCR model, from which parameters at independent camera trapping arrays ("sessions") can either be estimated separately or shared across sessions or groups to improve parameter estimation (Sutherland et al. 2019). All SCR analyses were performed in the R package oSCR (Sutherland et al. 2019).

SCR models consist of two sub-models: an ecological process model that describes the density and distribution of individual animals' activity centers within the sampling area (the state-space, i.e., the region that contains all individuals potentially exposed to sampling, which is defined by the researcher) and a spatially explicit **observation model** that describes the probability of detecting an animal at a trap based on the distance between its activity center during the sampling period and the trap location (Royle et al. 2013). Individual captures at multiple detectors provide information on the distribution of latent animal activity centers, which cannot be directly observed (Royle et al. 2013). The **baseline detection probability** (p0) describes the probability of detecting an individual if its activity center were situated exactly at the trap location. The **spatial scale parameter sigma** ($\sigma$) describes how rapidly detection probability declines with distance to the camera trap and is related to animal movement and home range size; it can be thought of as a proxy for home range size because for animals with small home ranges (small sigma) detection probability quickly declines as distance from a trap increases (Efford et al. 2009). **Density** (D), which is our main parameter of interest, is modeled as a spatial point process that describes the distribution of the latent activity centers in the state-space.

Details on specification of candidate sub-models for each parameter are listed in Table 1. Camera trapping grids were stratified by urbanization level (urb = Urban, Suburban, or Exurban)

based on percent impervious surface (see above). Datasets like this that contain a relatively low number of captures and spatial recaptures can present challenges for parameter estimation (Jared Laufenberg, *personal communication*). We therefore modeled parameters as functions of a categorical urbanization variable rather than a continuous impervious surface covariate because the latter presented challenges with model convergence. Grouping the trapping grids in this way enabled estimation of density and other parameters at the urbanization category level but precluded investigation of the influence of finer-scale spatial covariates. For detection probability, we fitted models containing a behavioral effect (b), urbanization category effect (urb), or both. Because camera traps were baited, an individual's detection probability at a trap may increase after the first capture (a "trap-happy" behavioral response.) Because sigma is often inversely related to baseline detection probability (Efford and Mowat 2014), we fitted candidate models allowing sigma to vary with urbanization category as well. We also evaluated models that included an effect of sex on sigma, since male cats typically have larger home range sizes than females (Hall et al. 2016). Model fit was assessed in an information theoretic approach and all models with $\Delta AIC \leq 2$ were considered equally plausible.

To specify the state-space, we used an approximation of sigma based on the mean maximum distance moved (MMDM) calculated from the summarized detection data (Table S2). For an idealized circular home range, a rough estimate of sigma can be calculated as approximately 0.5*MMDM (Sutherland et al. 2019). We specified state-spaces for each of the trapping grids using a buffer width of 500m, which is 4 times the largest session-specific approximation of sigma (~125m) to ensure that the state-space encompassed all individuals with a non-zero probability of being exposed to sampling. We set the state-space resolution, which should be less than sigma, at $50m^2$ (recommendation: ~0.5*sigma; Sutherland et al. 2019). We

also tested the influence of the state-space specification on parameter estimates by fitting intercept-only models with different buffer widths and pixel resolutions (Table S1).

**Table 1.** Candidate model specifications and descriptions of density (D), detection probability (p0), and sigma (sig)

| Model name | Model formulation | Description |
|---|---|---|
| m0 | D ~ 1, p0 ~ 1, sig ~ 1 | - Null model. Density, detection probability, and sigma are constant across sites |
| m1 | D ~ urb, p0 ~ 1, sig ~ 1 | - Density is function of urbanization category (urb)<br>- Detection probability and sigma constant across sites |
| m2 | D ~ urb, p0 ~ b, sig ~ sex | - Density is function of urbanization category<br>- Behavioral effect (b) for detection probability due to baiting: p0 depends on previous capture (trap-happy or trap-shy response)<br>- Sigma is function of sex (home range size varies by sex) |
| m3 | D ~ urb, p0 ~ b, sig ~ urb | - Density is function of urbanization category<br>- Behavioral effect for detection probability due to baiting<br>- Sigma is function of urbanization category: home range size depends on resource / habitat attributes that differ with urbanization |
| m4 | D ~ urb, p0 ~ urb, sig ~ urb | - All parameters are functions of urbanization category |
| m5 | D ~ urb, p0 ~ b, sig ~ sex + urb | - Density is function of urbanization category<br>- Behavioral effect for detection probability due to baiting<br>- Sigma is function of both sex and urbanization category |
| m6 | D ~ urb, p0 ~ b + urb, sig ~ sex + urb | - Full model: Density is function of urbanization category<br>- Detection probability is function of both behavioral effect and urbanization category<br>- Sigma is function of both sex and urbanization category |

## Results

### Camera Trapping

During the 2019 field season, we obtained 35,187 photos of cats across a total of 820 trap-nights. Of these, 967 (2.75%) were classified as “unmarked”; these were primarily all-black cats and

individuals whose coat color or pattern could not be determined from nighttime captures (orange and all-white cats are frequently indistinguishable in infrared photographs; Elizondo and Loss 2016, Cove et al. 2023). An additional 2,418 photos (6.87%) were classified as "marked but unidentified," when some markings could be observed but were not sufficient to confirm individual identity (common when only a portion of the animal was photographed). Both unidentified-marked and unmarked photographs were excluded from the analysis; a total of 90.4% of cat photos were useable.

Across the 16 trapping arrays, we identified 524 individual cats based on unique coat patterns and other physical characteristics and generated capture histories for each individual. Of these, 100 (19.1 %) were female, 150 (28.6%) were male, and 274 (52.3%) were of unknown sex. The number of unique individuals detected in each of the camera trapping arrays (sessions) ranged from 7 - 86, though the average number of spatial recaptures (detections of an individual at more than 1 camera trap, listed as "avg spatial caps") was relatively low (Table S2). Mean maximum distance moved ranged from 87m to 247m, with the pooled value across all grids 138m. Estimates of all parameters in the null model were relatively insensitive to state-space buffer size and pixel resolution, though density estimates were slightly higher for finer resolutions (Table S1).

Of the seven candidate models for cat density (Table 1), the full model (m6) was ranked highest and no subset models had $\Delta AIC < 2$ (Table 2). The top model allowed all three parameters (density, detection probability, and sigma) to vary as a function of urbanization class and also included a behavioral effect of baiting on baseline detection probability and an effect of sex on sigma.

**Table 2.** Support for candidate SCR models of cat density in San Juan, Puerto Rico.

| Model Name | Description | logLik | K | AIC | ΔAIC | Wt. | Cum. Wt. |
|---|---|---|---|---|---|---|---|
| m6* | D(~urb) p(~b + urb) sig(~sex + urb) | 3737.16 | 12 | 7498.33 | 0 | 1 | 1 |
| m5 | D(~urb) p(~b) sig(~sex + urb) | 3752.91 | 10 | 7525.82 | 27.5 | 0 | 1 |
| m3 | D(~urb) p(~b) sig(~urb) | 3762.39 | 9 | 7542.78 | 44.45 | 0 | 1 |
| m2 | D(~urb) p(~b) sig(~sex) | 3777.7 | 8 | 7571.39 | 73.07 | 0 | 1 |
| m4 | D(~urb) p(~urb) sig(~urb) | 3961.99 | 10 | 7943.98 | 445.66 | 0 | 1 |
| m1 | D(~urb) p(~1) sig(~1) | 4024.81 | 6 | 8061.62 | 563.3 | 0 | 1 |
| m0 (null) | D(~1) p(~1) sig(~1) | 4102.18 | 4 | 8212.37 | 714.04 | 0 | 1 |

* Urb = urban, suburban, or exurban; b = 0 or 1 (behavioral effect of previous capture at trap), sex = male or female (individuals of unknown sex not used to estimate sigma)

Model-estimated cat density (individuals per square kilometer; Table 3a and Fig. 2) differed substantially by urbanization category. As predicted, cat density was highest in urban areas (mean ± SE: 473 ± 40 cats/km$^2$), lowest in exurban areas, (48 ± 8 cats/ km$^2$), and intermediate in suburban sites (262 ± 23 cats/ km$^2$). Baiting had a strongly positive effect on baseline detection probability, p0 (Table 3b and Fig. 3). Baiting induces a local behavioral response so that detection probability at a given trap is higher after the individual has been detected there previously. Probability of first detection differed between the three urbanization categories, but in all cases detection probability at a trap increased if an individual had been detected previously (behavioral effect (b) = 0 for first capture, 1 for subsequent capture). While detection probability was lowest in exurban areas, suburban detection probability was unexpectedly highest overall. As with baseline detection probability, the scale parameter sigma (Table 3c and Fig. 5) differed by urbanization level. Sigma was larger for males than females in all three urbanization categories, reflecting larger male home range sizes. For both sexes, sigma was largest in exurban areas where both cat and human population density is lower (Fig. 5).

**Table 3.** Parameter estimates and 95% confidence intervals (lwr, upr) of detection probability (p0), scale / movement (sigma), and density (D) from the top-ranked model.

3a. Cat density by urbanization level

| Urbanization level | Density (cats/ km$^2$) | SE | lwr | upr |
|---|---|---|---|---|
| Urban | 473 | 40.12 | 401 | 559 |
| Suburban | 262 | 22.89 | 221 | 311 |
| Exurban | 48 | 8.2 | 34 | 67 |

3b. Baseline detection probability (p0) by urbanization level, showing behavioral effect of baiting

| Urbanization level | Behav. effect | Detection probability | SE | lwr | upr |
|---|---|---|---|---|---|
| Urban | No bait | 0.18 | 0.03 | 0.13 | 0.24 |
| Urban | Bait | 0.90 | 0.02 | 0.86 | 0.94 |
| Suburban | No bait | 0.59 | 0.1 | 0.40 | 0.76 |
| Suburban | Bait | 0.98 | 0.01 | 0.96 | 0.99 |
| Exurban | No bait | 0.09 | 0.02 | 0.06 | 0.14 |
| Exurban | Bait | 0.81 | 0.05 | 0.68 | 0.89 |

3c. Scale parameter (sigma) by urbanization level and sex

| Urbanization level | Sex | Sigma (m) | SE | lwr | upr |
|---|---|---|---|---|---|
| Urban | Female | 45.10 | 2.66 | 40.17 | 50.62 |
| Urban | Male | 73.78 | 4.47 | 65.51 | 83.09 |
| Suburban | Female | 32.84 | 2.02 | 29.11 | 37.05 |
| Suburban | Male | 53.72 | 2.29 | 49.41 | 58.41 |
| Exurban | Female | 100.17 | 8.37 | 85.04 | 117.98 |
| Exurban | Male | 163.87 | 14.96 | 137.03 | 195.97 |

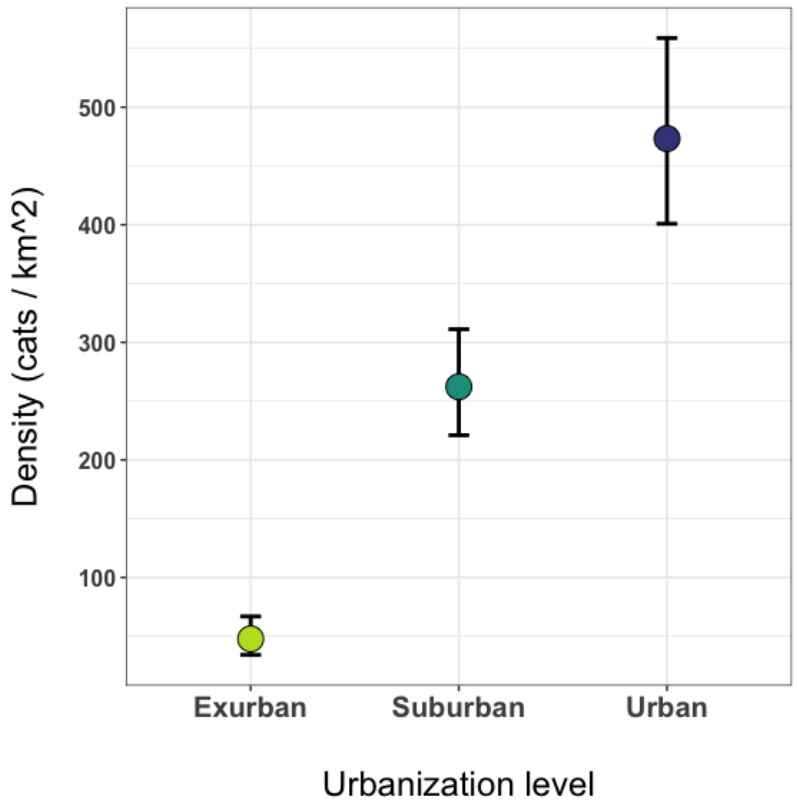


**Fig. 2.** Model estimates of free-roaming cat density per square kilometer for exurban, suburban, and urban areas of San Juan. Bars show 95% confidence intervals.

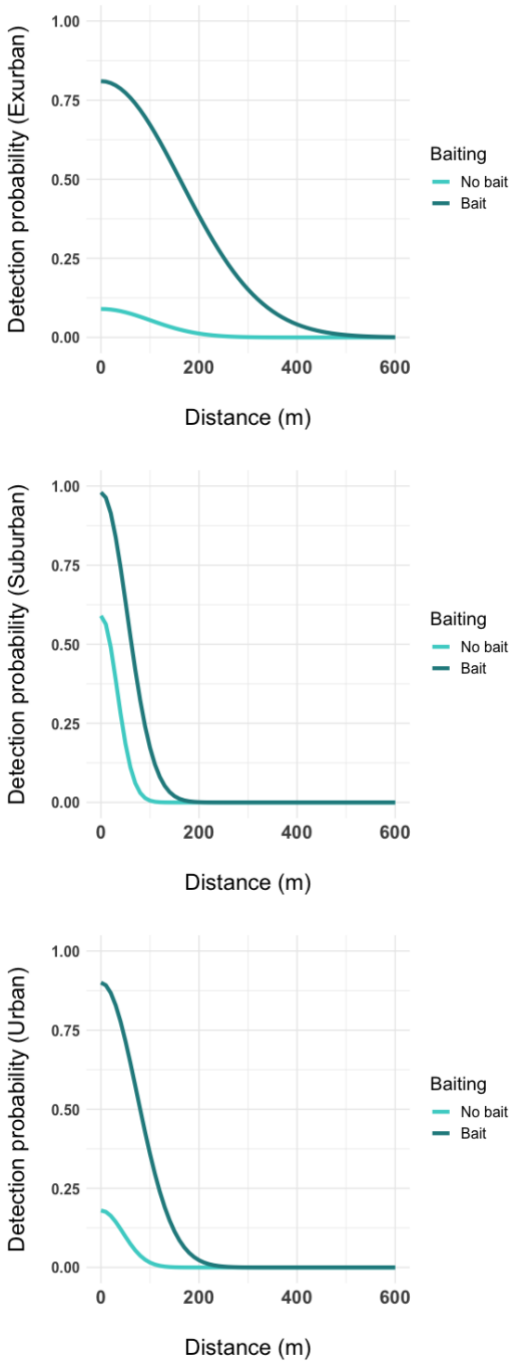


**Fig. 3.** Half-normal detection probability functions for the three urbanization levels. Estimated baseline detection probability (p0) is the y-intercept on each plot, with colors denoting the effect of a positive behavioral response to baiting on probability of detection. Note that for all sites detection probability increased with baiting, but the magnitude of the increase differed by urbanization category. Sigma, the scale or movement parameter, controls the "shoulder" of the curve: i.e., how rapidly detection probability decreases with distance from the trap location. Sigma also varied by urbanization level, reflecting relative differences in animal home range size.

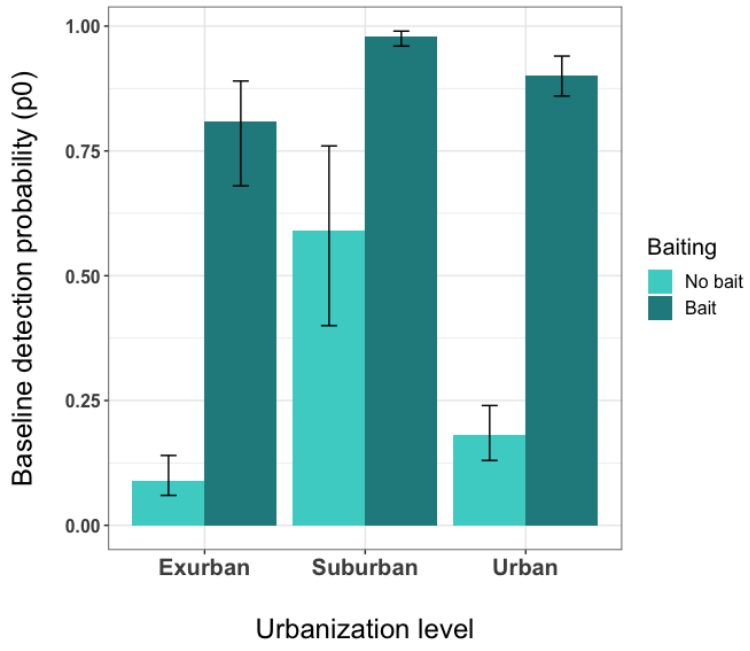


**Fig. 4.** Effect of baiting on baseline detection probability (p0). Error bars represent 95% confidence intervals.

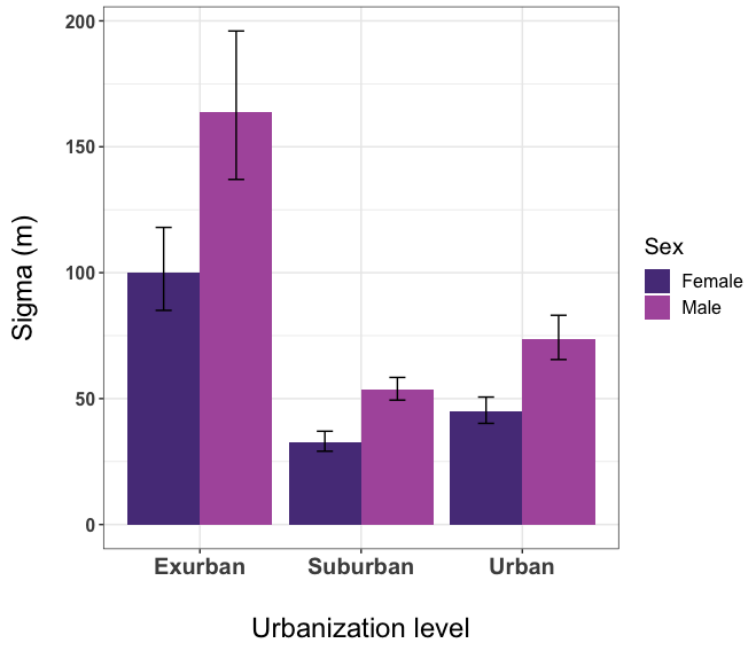


**Fig. 5**. Scale parameter, sigma, by sex and urbanization level. While the magnitudes differed, sigma is higher for males than females at all levels of urbanization, reflecting relative differences in animal home range size. Error bars represent 95% confidence intervals.

## Discussion

This study provides estimates of the density and distribution of free-roaming domestic cats across a gradient of urbanization in a Neotropical city, information that is necessary to evaluate if cats pose a threat to specific conservation priority bird species in Puerto Rico, and if so, where to allocate limited resources for population management (García et al. 2005b, Nytch et al. 2015). These quantities can help conservation practitioners identify where the potential negative impacts of free-roaming cats on wildlife and public health may be greatest, and where management might be targeted (Tulloch et al. 2015, Buchan et al. 2022). Both cat abundance and the feasibility of different cat management options can vary based on ecological, cultural, and socioeconomic factors (Wald et al. 2013, Dias et al. 2017, Lepczyk et al. 2022), requiring that population management and wildlife conservation plans be tailored to the system and region of interest. Establishing baseline population abundance or density is also required to assess if future cat management programs are meeting their stated objectives (Cove et al. 2023).

Our cat density estimates from San Juan, Puerto Rico fall within the range of values reported in both temperate and non-temperate regions of the world. Estimates of free-roaming cat density in the literature vary widely, reflecting both survey method and differences in ecological, biogeographical, and socioeconomic influences on cat abundance and distribution (Des Roches et al. 2021), as well as challenges inherent to surveying a nocturnal, domesticated predator in anthropogenic environments (Bateman and Fleming 2012). A 2013 visual survey in the historic district of Old San Juan (Castro-Prieto and Andrade-Núñez 2018) estimated free-roaming cat densities at 360 cats/km$^2$, which is somewhat lower than our estimate of 473 ± 40 cats/ km$^2$ for urban San Juan but within the same order of magnitude. A comprehensive review of cat management efforts on islands (Nogales et al. 2004) listed an estimated density of 243 cats/km$^2$

on the island of Cousine in the Seychelles (similar to our estimate for suburban areas of San Juan), but the majority of island studies reported fewer than 79 cats/km$^2$. More recently, Dias et al. (2017) combined distance sampling and resident surveys to estimate cat density on Fernando de Noronha Island off the coast of Brazil at 71.1 cats/km$^2$, and Hwang et al. (2018) reported densities of 132 - 268 free-roaming cats/km$^2$ in Seoul, South Korea.

Although we found higher densities than many other island studies, our estimates were lower than those obtained using different survey methods in several temperate cities. For example, researchers estimated densities ranging from 0 - 4,940 cats/km$^2$ in Guelph, Ontario, Canada (total population of 7662 (95% CI: 6145 - 9966) in the 86.7 km$^2$ city area) using distance sampling, with spatial patterns reflecting increased feeding and breeding opportunities in residential and industrial areas (Flockhart et al. 2016b). In urban regions of Britain, density estimates based on household surveys ranged from 132 - 1,580 cats/km$^2$ (Sims et al. 2008). Direct counts yielded estimates of 1,200 - 1,950 cats/km$^2$ in Rome, Italy (Natoli 1985), between 2,300 - 2,800 cats/ km$^2$ in Jerusalem, Israel (Mirmovitch 1995), and 3,100 cats/km$^2$ in Nagasaki, Japan (Izawa et al. 1991). Other studies have obtained dramatically lower estimates: in southern Florida, which is comparable in climate to parts of Puerto Rico, cat densities based on camera trapping were low (1.27 - 4.79 cats/km$^2$), likely reflecting low human population density across much of the study area combined with targeted cat removal efforts (Cove et al. 2018).

As expected, sigma was largest in exurban areas where both cat and human population density is lower (Fig. 5). While we observed residents feeding free-roaming cats throughout the municipality, it was especially prevalent in suburban and urban sites. Cats may range more widely to find food if they receive less provisioning (intentional or unintentional) from humans. In addition, exurban areas in San Juan are often characterized by large yards, small pastures, and

agricultural plots (Ramos-González 2014, Martinuzzi et al. 2018) that are relatively permeable to cats and other animals. In contrast, movements may be more constrained in urban and suburban areas due to "hard edged" barriers imposed by buildings, walls, and busy roads. Contrary to our expectations, sigma was lower in the suburbs than urban areas. While we were unable to determine what proportion of cats in our study were owner versus unowned, sigma is related to home range size and might reflect more localized movements of pet cats around their homes (Kays et al. 2020). This is also consistent with the expectation that sterilization reduces roaming behavior (Hall et al. 2016) and that owned cats are more likely to be sterilized than unowned individuals.

While camera trapping combined with spatial capture-recapture modeling is particularly useful for studying animals whose life history attributes and behavior make direct observation difficult (for example, nocturnal, cryptic, or wary species or those living in challenging terrain), there are several limitations in their application to free-roaming cats, particularly in urban environments. Researchers studying tigers *(Panthera tigris)* were the first to develop the technique of estimating animal abundance from photographic captures of naturally marked individuals *(*Karanth 1995, Karanth and Nichols 1998). Endangered species and apex predators such as wild felids typically occur in low densities, meaning that a limited number of individuals are captured in a particular study area and identification is generally not complicated by volume (O'Connell et al. 2011). In contrast, free-roaming cats frequently achieve high densities in human-dominated landscapes, presenting challenges when dozens of individuals must be distinguished at a trapping grid or at a single camera. While the wide variety of domestic cat coat colors and patterns lends itself to individual recognition, certain individuals may be permanently unmarked (e.g., black cats and other uniform colors) or "facultatively" unmarked (the "orange

tabby problem" where certain coat patterns are indistinguishable in nocturnal infrared photographs, described by Elizondo and Loss (2016). Researchers have developed sophisticated modeling techniques to address such "partially unmarked" populations (Augustine et al. 2018a, b; Cove et al. 2023), but they can be challenging for non-statisticians to implement. However, photo classification via machine learning and crowdsourcing approaches increasingly allow research teams to process large volumes of camera trap data (e.g., Swanson et al. 2015, Cove et al. 2021, Norouzzadeh et al. 2021, Lasky et al. 2021). While accurate identification of individuals has historically lagged behind species-level identification with these techniques, it will undoubtedly improve in the future (Tuia et al. 2022).

Camera trapping in urban environments presents a unique set of logistical challenges and opportunities (Herrera et al. 2021). We worked closely with residents in San Juan to explain project objectives and obtain permission to install cameras on private property. Most community members were interested and supportive of the research and we had minimal issues with camera theft or vandalism. More challenging were the spatial limitations of installing camera arrays in the built environment and the high volumes of non-cat images generated by vehicle traffic and other domestic animals and wildlife attracted to baited traps. Baiting was necessary to obtain sufficient photographic captures and recaptures in a short time window (O'Connell et al. 2011), but a longer study period would have likely increased the number of spatial recaptures and perhaps allowed us to eliminate or reduce the frequency of baiting, thereby reducing non-target captures.

**Conservation and Management**

Introduced species such as domestic cats, and the ecological and economic damages they incur, are part of the global footprint of European colonialism (Dyer et al. 2017, Lenzner et al.

2022; Raja 2022). Though the exact date of their introduction to the Americas is unknown, domestic cats probably arrived on ships where they were used to control rats and mice (Driscoll et al. 2009). While still used for pest control in some cases, domestic cats are more often viewed as pets and companions than as working animals. However, some farmers in Puerto Rico encourage free-roaming cats and dogs to help control crop damage from introduced green iguanas (*Iguana iguana*) (Villanueva et al. 2022). During informal conversations with homeowners, we encountered a variety of perspectives on San Juan's free-roaming cat population. Several residents reported that they valued cats for their perceived ability to hunt rats (*Rattus* sp.) and mice (*Mus musculus*), both of which have also been introduced to the island (García et al. 2005a). Other residents opposed free-roaming cats and the maintenance of feral colonies in particular, citing concerns about fecal deposition, disease transmission, fighting, and animal welfare.

The harmful impacts of free-roaming cat predation are well-supported by an extensive body of scientific literature (reviewed in Loss et al. 2022), and evidence of their nonlethal effects continues to rise. However, management of free-roaming cats is complicated by human values and attitudes towards this species, as well as persistent disinformation from certain advocacy groups (Loss and Marra 2018) and underrepresentation of scientists' viewpoints in media coverage of the topic (Gow et al. 2022). The management of introduced species is frequently complex and requires a substantial investment in public engagement, trust, and education to be successful (Crowley et al. 2017, Beever et al. 2019). This is especially so for the domestic cat, a charismatic species that is also a beloved pet and valued companion for millions of people worldwide (Driscoll et al. 2009).

Studies like ours are one piece of the puzzle when it comes to both understanding and mitigating cat impacts on birds and other wildlife. For example, we currently have little information about which bird species in Puerto Rico free-roaming cats prey upon or how their diet varies spatially. Coupling information on cat space use with detailed diet analysis is essential to establish which species cats prey upon and where (Castañeda et al. 2019). Outside of San Juan, free-roaming cats have been identified as potential threats to endangered bird species like the Puerto Rican Parrot (Engeman et al. 2003, 2006) and occur even in protected areas such as El Yunque National Forest (Zimmerman et al. 2021) and the Caribbean National Forest (Blundell et al. 2003). Free-roaming cats have been documented killing multiple bat species at a cave in Puerto Rico (Rodríguez-Durán et al. 2010), which the authors suggest might also threaten the endangered Puerto Rican boa (*Epicrates inornatus*) through prey depletion, if not direct predation (Rodríguez-Durán 1996). Endemic Puerto Rican crested anoles (*Anolis cristellatus*) display higher rates of caudal autotomy in urban areas, which likely reflects more predation attempts by cats and other introduced mammals (Tyler et al. 2016). Cats may also prey upon Puerto Rico's introduced fauna, which includes over 30 non-native bird species in addition to introduced mammals, reptiles, and amphibians (Henderson 1992, Miller and Lugo 2009, Finch et al. 2010, Falcón and Tremblay 2018, Zimmerman et al. 2021, Villanueva et al. 2022). This may be an important consideration for conservation managers because efforts to control one invasive prey species without simultaneous management of others can result in unintended negative secondary impacts on wildlife and ecosystems (Courchamp et al. 1999, 2003; Zavaleta et al. 2001, Bergstrom et al. 2009).

While the heart of San Juan is heavily urbanized, the San Juan metropolitan area nonetheless hosts a variety of both small and large green spaces that offer habitat for native

birds, reptiles, and amphibians (Martinuzzi et al. 2007, 2018; Ramos-González 2014). Even small reserves in Puerto Rico often protect a high diversity of species and habitat types (Castro-Prieto et al. 2016). Neotropical cities can provide important year-round habitat for resident bird species (Ortega-Álvarez and MacGregor-Fors 2009, Puga-Caballero et al. 2014, Escobar-Ibáñez et al. 2020) as well as valuable stopover and non-breeding season habitat for Nearctic-Neotropical migrants (MacGregor-Fors et al. 2010, Amaya-Espinel and Hostetler 2019, Pacheco-Muñoz et al. 2022b, a). During fieldwork, we detected both endemic and migratory bird species throughout the San Juan metropolitan area, particularly in suburban and exurban neighborhoods. While urban areas in northeast Puerto Rico tend to be dominated by high numbers of introduced bird species, endemic species may persist in less developed areas (Vázquez-Plass and Wunderle, Jr. 2013). This may indicate that, although cats reach their highest densities in the most developed urban areas of San Juan, their potential impacts on native avifauna may be greater in the suburbs, exurbs, and protected green spaces; these areas should be prioritized for future research and management.

**Acknowledgments**

I owe an immense debt of gratitude to field technicians Emilio Font Nicole and Noraisha Bonilla, without whom this project would not have been possible. Their contributions to the study design, data collection, neighborhood outreach, and translations were invaluable, as were the many discussions about free-roaming cats, wildlife, and Puerto Rican culture. I am especially grateful for the interest and kindness of the many San Juan residents who generously allowed us to install trail cameras in their neighborhoods, shared their perspectives on free-roaming cats, and patiently listened to questions in my earnest but rudimentary Spanish. Jared Laufenberg of the U.S. Fish and Wildlife Service provided invaluable modeling assistance. Funding for this

research was provided by a Blake-Nuttall Fund Grant from the Nuttall Ornithological Club, the Florida Ornithological Society Robertson Fellowship, the ABC Humane Wildlife Women in STEM scholarship, and UMCES Appalachian Laboratory Student Research Project and Travel Awards.

## Chapter 4 Supplemental Information

**Table S1.** Sensitivity of parameter estimates to formulation of state-space

| **State-space specification (m)** | | **Parameter estimates [95% CI] Intercept-only model: D~1, P0~1, sig~1** | | |
|---|---|---|---|---|
| **Buffer** | **Resolution** | **Density (cats/km$^2$)** | **Detection probability** | **Scale parameter** |
| 500 | 20 | 198 [170, 231] | 0.92 [0.86 - 0.95] | 45.3 [44.1, 46.6] |
| 500 | 35 | 198 [170, 231] | 0.91 [0.86, 0.95] | 45.4 [44.2, 46.7] |
| 500 | 50 | 193 [166, 225] | 0.89 [0.84, 0.92] | 46.8 [45.5, 48] |
| 500 | 60 | 193 [166, 225] | 0.86 [0.82, 0.90] | 47.0 [45.8, 48.3] |
| 400 | 50 | 193 [166, 225] | 0.89 [0.84, 0.92] | 46.8 [45.5, 48.0] |
| 300 | 50 | 193 [166, 225] | 0.89 [0.84, 0.92] | 46.7 [45.5, 48.0] |

**Table S2.** Capture summaries for the 16 camera trapping grids ("sessions"), labeled S1-S16, listing the number of unique individuals detected in each grid and number of traps and occasions per grid. Average captures ("avg caps") is the number of times each individual was detected in the grid, while average spatial recaptures ("avg spatial caps") is the number of captures at >1 detector. Mean maximum distance moved (MMDM) is estimated separately for each grid as well as across grids (pooled MMDM).

```
> sf_new3

             S1 S2 S3 S4 S5 S6 S7 S8 S9 S10 S11 S12 S13 S14 S15 S16
n individuals 16 12  7 59 32 39  7 29 18  39  86  45  66  16  25  28
n traps       10  9  9  9  8 10  9  8  9   9  10   8   9   9  10   8
n occasions   11 10  7  7 11  7 11  7  9   7   7   7  11   7   7   7

                    S1     S2     S3     S4     S5     S6     S7     S8     S9    S10   S11    S12   S13    S14    S15    S16
avg caps          3.56   5.00   4.29   3.41   4.56   3.90   4.00   6.28   4.17   3.95  4.33   4.02  4.30   4.88   3.80   3.64
avg spatial caps  1.31   1.75   2.00   1.15   1.84   1.36   1.86   1.62   1.56   1.46  1.23   1.27  1.36   1.81   1.28   1.18
mmdm            155.94 177.26 180.29 127.82 134.87 159.72 115.40 162.74 113.70 190.67 91.13 139.62 87.77 247.15 118.92 141.48

Pooled MMDM:  137.95
```


**Fig. S1.** A single free-roaming cat photographed at two different trail camera locations in an exurban trapping grid.

# Bibliography


Abrahms, B., E. O. Aikens, J. B. Armstrong, W. W. Deacy, M. J. Kauffman, and J. A. Merkle (2021). Emerging Perspectives on Resource Tracking and Animal Movement Ecology. Trends in Ecology & Evolution 36:308–320.

Adalsteinsson, S. A., J. J. Buler, J. L. Bowman, V. D'Amico, Z. S. Ladin, and W. G. Shriver (2018). Post-independence mortality of juveniles is driven by anthropogenic hazards for two passerines in an urban landscape. Journal of Avian Biology 49:e01555.

Aegerter, J., D. Fouracre, and G. C. Smith (2017). A first estimate of the structure and density of the populations of pet cats and dogs across Great Britain. PLOS ONE 12:e0174709.

Agudelo-Álvarez, L., J. Moreno-Velasquez, and N. Ocampo-Peñuela (2010). Colisiones de aves contra ventanales en un campus universitario de Bogotá, Colombia. Ornitología Colombiana:3–10.

Aguirre, A. A., T. Longcore, M. Barbieri, H. Dabritz, D. Hill, P. N. Klein, C. Lepczyk, E. L. Lilly, R. McLeod, J. Milcarsky, C. E. Murphy, et al. (2019). The One Health Approach to Toxoplasmosis: Epidemiology, Control, and Prevention Strategies. EcoHealth 16:378–390.

Ahola, M., T. Laaksonen, K. Sippola, T. Eeva, K. Rainio, and E. Lehikoinen (2004). Variation in climate warming along the migration route uncouples arrival and breeding dates. Global Change Biology 10:1610–1617.

Aikens, E. O., I. D. Bontekoe, L. Blumenstiel, A. Schlicksupp, and A. Flack (2022). Viewing animal migration through a social lens. Trends in Ecology & Evolution:S0169534722001410.

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and K. L. Monteith (2017). The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Åkesson, S., and A. Hedenström (2007). How migrants get there: Migratory performance and orientation. BioScience 57:123–133.

Åkesson, S., and B. Helm (2020). Endogenous programs and flexibility in bird migration. Frontiers in Ecology and Evolution 8:78.

Alerstam, T. (2001). Detours in Bird Migration. Journal of Theoretical Biology 209:319–331.

Alerstam, T. (2011). Optimal bird migration revisited. Journal of Ornithology 152:5–23.

Alerstam, T., A. Hedenström, and S. Åkesson (2003). Long-distance migration: evolution and determinants. Oikos 103:247–260.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: the relative importance of time, energy, and safety. In Bird Migration (E. Gwinner, Editor). Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 331–351.

Amano, T., T. Székely, K. Koyama, H. Amano, and W. J. Sutherland (2010). A framework for monitoring the status of populations: An example from wader populations in the East Asian–Australasian flyway. Biological Conservation 143:2238–2247.

Amaya-Espinel, J. D., and M. E. Hostetler (2019). The value of small forest fragments and urban tree canopy for Neotropical migrant birds during winter and migration seasons in Latin American countries: A systematic review. Landscape and Urban Planning 190:103592.

Amélineau, F., C. Péron, A. Lescroël, M. Authier, P. Provost, and D. Grémillet (2014). Windscape and tortuosity shape the flight costs of northern gannets. Journal of Experimental Biology 217:876–885.

Anadón-Irizarry, V., J. Corven, V. Méndez-Gallardo, J. A. Salguero-Faría, and J. Schwagerl (2009). Puerto Rico and U.S. Unincorporated Territories. In Important Bird Areas Americas - Priority sites for biodiversity conservation (C. Devenish, D. F. Días Fernández, R. P. Clay, I. Davidson and I. Yépez Zabala, Editors). Birdlife International, Quito, Ecuador, pp. 317–328.

Arcilla, N., C. Y. Choi, K. Ozaki, and C. A. Lepczyk (2015). Invasive species and Pacific island bird conservation: a selective review of recent research featuring case studies of Swinhoe's storm petrel and the Okinawa and Guam rail. Journal of Ornithology 156:S199–S207.

Arévalo, J. E., and K. Newhard (2011). Traffic noise affects forest bird species in a protected tropical forest. Revista de Biología Tropical 59:969–980.

Arias, P., N. Bellouin, E. Coppola, R. Jones, G. Krinner, J. Marotzke, V. Naik, M. Palmer, G.-K. Plattner, J. Rogelj, M. Rojas, et al. (2021). Technical Summary. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 37–118.

Arizaga, J., E. Unamuno, O. Clarabuch, and A. Azkona (2013). The impact of an invasive exotic bush on the stopover ecology of migrant passerines. Animal Biodiversity and Conservation 36:1–11.

Armstrong, J. B., G. Takimoto, D. E. Schindler, M. M. Hayes, and M. J. Kauffman (2016). Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97:1099–1112.

Aronson, M. F., C. A. Lepczyk, K. L. Evans, M. A. Goddard, S. B. Lerman, J. S. MacIvor, C. H. Nilon, and T. Vargo (2017). Biodiversity in the city: key challenges for urban green space management. Frontiers in Ecology and the Environment 15:189–196.

van Asch, M., and M. E. Visser (2007). Phenology of Forest Caterpillars and Their Host Trees: The Importance of Synchrony. Annual Review of Entomology 52:37–55.

Ash, S. J., and C. E. Adams (2003). Public Preferences for Free-Ranging Domestic Cat (Felis catus) Management Options. Wildlife Society Bulletin (1973-2006) 31:334–339.

Augspurger, T., M. R. Smith, C. U. Meteyer, and K. A. Converse (1996). Mortality of passerines adjacent to a North Carolina corn field treated with granular carbofuran. Journal of Wildlife Diseases 32:113–116.

Augustine, B. C., J. A. Royle, M. J. Kelly, C. B. Satter, R. S. Alonso, E. E. Boydston, and K. R. Crooks (2018a). Spatial capture–recapture with partial identity: An application to camera traps. The Annals of Applied Statistics 12.

Augustine, B. C., F. E. C. Stewart, J. A. Royle, J. T. Fisher, and M. J. Kelly (2018b). Spatial Mark-Resight for Categorically Marked Populations with an Application to Genetic Capture-Recapture. Ecology.

Ault, T. R., M. D. Schwartz, R. Zurita-Milla, J. F. Weltzin, and J. L. Betancourt (2015). Trends and Natural Variability of Spring Onset in the Coterminous United States as Evaluated by a New Gridded Dataset of Spring Indices. Journal of Climate 28:8363–8378.

Bairlein, F. (2016). Migratory birds under threat. Science 354:547–548.

Bairlein, F., and E. Gwinner (1994). Nutritional Mechanisms and Temporal Control of Migratory Energy Accumulation in Birds. Annual Review of Nutrition 14:187–215.

Bairlein, F., and O. Hüppop (2004). Migratory Fuelling and Global Climate Change. In Advances in Ecological Research. Academic Press, pp. 33–47.

Baker, P. J., A. J. Bentley, R. J. Ansell, and S. Harris (2005). Impact of predation by domestic cats Felis catus in an urban area. Mammal Review 35:302–312.

Balogh, A. L., T. B. Ryder, and P. P. Marra (2011). Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats. Journal of Ornithology 152:717–726.

Bamber, R. C., and E. C. Herdman (1927). The inheritance of black, yellow and tortoiseshell coat-colour in cats. Journal of Genetics 18:87–97.

Barber, J. R., C. L. Burdett, S. E. Reed, K. A. Warner, C. Formichella, K. R. Crooks, D. M. Theobald, and K. M. Fristrup (2011). Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. Landscape Ecology 26:1281.

Barmentlo, S. H., M. Schrama, G. R. de Snoo, P. M. van Bodegom, A. van Nieuwenhuijzen, and M. G. Vijver (2021). Experimental evidence for neonicotinoid driven decline in aquatic emerging insects. Proceedings of the National Academy of Sciences 118:e2105692118.

Barshep, Y., A. Hedenström, and L. G. Underhill (2011). Impact of Climate and Predation on Autumn Migration of the Curlew Sandpiper. Waterbirds 34:1–9.

Bateman, B. L., L. Taylor, C. Wilsey, J. Wu, G. S. LeBaron, and G. Langham (2020). Risk to North American birds from climate change-related threats. Conservation Science and Practice 2:e243.

Bateman, P. W., and P. A. Fleming (2012). Big city life: carnivores in urban environments. Journal of Zoology 287:1–23.

Bates, D., M. Maechler, B. M. Bolker, and S. Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67(1):1–48.

Bauer, S., and M. Klaassen (2013). Mechanistic models of animal migration behaviour – their diversity, structure and use. Journal of Animal Ecology 82:498–508.

Bauer, S., J. M. McNamara, and Z. Barta (2020). Environmental variability, reliability of information and the timing of migration. Proceedings of the Royal Society B: Biological Sciences 287:20200622.

Bauer, S., J. Shamoun-Baranes, C. Nilsson, A. Farnsworth, J. F. Kelly, D. R. Reynolds, A. M. Dokter, J. F. Krauel, L. B. Petterson, K. G. Horton, and J. W. Chapman (2019). The grand challenges of migration ecology that radar aeroecology can help answer. Ecography 42:861–875.

Bayly, N. J., C. Gómez, K. A. Hobson, and K. V. Rosenberg (2016). Prioritizing tropical habitats for long-distance migratory songbirds: an assessment of habitat quality at a stopover site in Colombia. Avian Conservation and Ecology 11:art5.

Bayly, N. J., K. V. Rosenberg, W. E. Easton, C. Gómez, J. Carlisle, D. N. Ewert, A. Drake, and L. Goodrich (2018). Major stopover regions and migratory bottlenecks for Nearctic-Neotropical landbirds within the Neotropics: a review. Bird Conservation International 28:1–26.

Beever, E. A., D. Simberloff, S. L. Crowley, R. Al-Chokhachy, H. A. Jackson, and S. L. Petersen (2019). Social–ecological mismatches create conservation challenges in introduced species management. Frontiers in Ecology and the Environment 17:117–125.

Bellard, C., C. Marino, and F. Courchamp (2022). Ranking threats to biodiversity and why it doesn't matter. Nature Communications 13:2616.

Bennett, K. F. P., B. S. Evans, J. A. Clark, and P. P. Marra (2021). Domestic Cat Abundance and Activity Across a Residential Land Use Gradient. Frontiers in Ecology and Evolution 9:643845.

Bennett, R. E., A. D. Rodewald, K. V. Rosenberg, R. Chandler, L. Chavarria-Duriaux, J. A. Gerwin, D. I. King, and J. L. Larkin (2019). Drivers of variation in migration behavior for a linked population of long-distance migratory passerine. The Auk 136:ukz051.

Benton, T. G., D. M. Bryant, L. Cole, and H. Q. Crick (2002). Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of applied ecology 39:673–687.

Bergstrom, D. M., A. Lucieer, K. Kiefer, J. Wasley, L. Belbin, T. K. Pedersen, and S. L. Chown (2009). Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46:73–81.

Bernanke, J., and H.-R. Köhler (2009). The Impact of Environmental Chemicals on Wildlife Vertebrates. In Reviews of Environmental Contamination and Toxicology (D. M. Whitacre, Editor). Springer, New York, NY, pp. 1–47.

Bernard, R. F. (1966). DDT residues in avian tissues. Journal of Applied Ecology:193–198.

Bernardino, J., K. Bevanger, R. Barrientos, J. F. Dwyer, A. T. Marques, R. C. Martins, J. M. Shaw, J. P. Silva, and F. Moreira (2018). Bird collisions with power lines: State of the art and priority areas for research. Biological Conservation 222:1–13.

Besterman, A. F., S. M. Karpanty, and M. L. Pace (2020). Impact of exotic macroalga on shorebirds varies with foraging specialization and spatial scale. PLOS ONE 15:e0231337.

Beyer, W. N., J. C. Franson, J. B. French, T. May, B. A. Rattner, V. I. Shearn-Bochsler, S. E. Warner, J. Weber, and D. Mosby (2013). Toxic Exposure of Songbirds to Lead in the Southeast Missouri Lead Mining District. Archives of Environmental Contamination and Toxicology 65:598–610.

Bianchini, K., and C. A. Morrissey (2018). Assessment of Shorebird Migratory Fueling Physiology and Departure Timing in Relation to Polycyclic Aromatic Hydrocarbon Contamination in the Gulf of Mexico. Environmental Science & Technology 52:13562–13573.

Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg (2020). Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Bing, G.-C., C.-Y. Choi, H.-Y. Nam, J.-G. Park, G.-P. Hong, S.-J. Kim, H.-Y. Chae, and Y.-B. Choi (2012). Causes of Mortality in Birds at Stopover Island. Korean Journal of Ornithology.

Birds Canada (2022). motus: Fetch and use data from the Motus Wildlife Tracking System. [Online.] Available at https://motusWTS.github.io/motus.

Birnie-Gauvin, K., R. J. Lennox, C. G. Guglielmo, A. K. Teffer, G. T. Crossin, D. R. Norris, K. Aarestrup, and S. J. Cooke (2020). The Value of Experimental Approaches in Migration Biology. Physiological and Biochemical Zoology 93:210–226.

Bischof, R., N. R. Hansen, Ø. S. Nyheim, A. Kisen, L. Prestmoen, and T. Haugaasen (2022). Mapping the “catscape” formed by a population of pet cats with outdoor access. Scientific Reports 12:5964.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, A. Mysterud, A. E. J.-M. Gaillard, and E. M. A. McPeek (2012). A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? The American Naturalist 180:407–424.

Bjorge, R. R. (1987). Bird kill at an oil industry flare stack in northwest Alberta. Can. Field Nat.; (Canada) 101:3.

Blancher, P. (2013a). Estimated Number of Birds Killed by House Cats (Felis catus) in Canada. Avian Conservation and Ecology 8:art3.

Blancher, P. (2013b). Estimated Number of Birds Killed by House Cats (Felis catus) in Canada. Avian Conservation and Ecology 8:art3.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan (2013). Climate Change and the Past, Present, and Future of Biotic Interactions. Science 341:499–504.

Blundell, A. G., F. N. Scatena, R. Wentsel, and W. Sommers (2003). Ecorisk Assessment Using Indicators of Sustainability: Invasive Species in the Caribbean National Forest of Puerto Rico. 6.

Bolser, J. A., R. R. Alan, A. D. Smith, L. Y. Li, N. P. Seeram, and S. R. McWilliams (2013). BIRDS SELECT FRUITS WITH MORE ANTHOCYANINS AND PHENOLIC COMPOUNDS DURING AUTUMN MIGRATION. Wilson Journal of Ornithology 125:97–108.

Bonnaud, E., F. M. Medina, E. Vidal, M. Nogales, B. Tershy, E. Zavaleta, C. J. Donlan, B. Keitt, M. Le Corre, and S. V. Horwath (2011). The diet of feral cats on islands: a review and a call for more studies. Biological Invasions 13:581–603.

Bonnington, C., K. J. Gaston, and K. L. Evans (2013a). Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. Journal of Applied Ecology 50:15–24.

Bonnington, C., K. J. Gaston, and K. L. Evans (2013b). Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. Journal of Applied Ecology 50:15–24.

Borchers, D. L., and M. G. Efford (2008). Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies. Biometrics 64:377–385.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser (2006). Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

Bowler, D. E., A. D. Bjorkman, M. Dornelas, I. H. Myers-Smith, L. M. Navarro, A. Niamir, S. R. Supp, C. Waldock, M. Winter, M. Vellend, S. A. Blowes, et al. (2020). Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. People and Nature 2:380–394.

Bowler, D. E., H. Heldbjerg, A. D. Fox, M. de Jong, and K. Böhning-Gaese (2019). Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology 33:1120–1130.

Bowlin, M. S. (2005). Biotelemetry of New World thrushes during migration: Physiology, energetics and orientation in the wild. Integrative and Comparative Biology 45:295–304.

Bowlin, M. S., I.-A. Bisson, J. Shamoun-Baranes, J. D. Reichard, N. Sapir, P. P. Marra, T. H. Kunz, D. S. Wilcove, A. Hedenstrom, C. G. Guglielmo, S. Akesson, et al. (2010). Grand Challenges in Migration Biology. Integrative and Comparative Biology 50:261–279.

Bowman, D. M. J. S., J. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D'Antonio, R. DeFries, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, et al. (2011). The human dimension of fire regimes on Earth. Journal of Biogeography 38:2223–2236.

Breheny, P., and W. Burchett (2017). Visualization of Regression Models Using visreg. The R Journal 9.

Briedis, M., S. Hahn, and P. Adamík (2017). Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. BMC Ecology 17:11.

Brochet, A.-L., W. V. D. Bossche, V. R. Jones, H. Arnardottir, D. Damoc, M. Demko, G. Driessens, K. Flensted, M. Gerber, M. Ghasabyan, D. Gradinarov, et al. (2019). Illegal killing and taking of birds in Europe outside the Mediterranean: assessing the scope and scale of a complex issue. Bird Conservation International 29:10–40.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw (2008). Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23:453–460.

Brown de Colstoun, E. C., C. Huang, P. Wang, J. C. Tilton, B. Tan, J. Phillips, S. Niemczura, P.-Y. Ling, and R. E. Wolfe (2017). Global Man-made Impervious Surface (GMIS) Dataset From Landsat. [Online.] Available at https://doi.org/10.7927/H4P55KKF.

Buchan, C., A. M. A. Franco, I. Catry, A. Gamero, A. Klvaňová, and J. J. Gilroy (2022). Spatially explicit risk mapping reveals direct anthropogenic impacts on migratory birds. Global Ecology and Biogeography n/a.

Buehler, D. M., and T. Piersma (2008). Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. Philosophical Transactions of the Royal Society B: Biological Sciences 363:247–266.

Buler, J. J., and D. K. Dawson (2014). Radar analysis of fall bird migration stopover sites in the northeastern U.S. The Condor 116:357–370.

Buler, J. J., and F. R. Moore (2011). Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. Journal of Ornithology 152:101–112.

Burger, J., N. Tsipoura, L. J. Niles, M. Gochfeld, A. Dey, and D. Mizrahi (2015). Mercury, lead, cadmium, arsenic, chromium and selenium in feathers of shorebirds during migrating through Delaware Bay, New Jersey: comparing the 1990s and 2011/2012. Toxics 3:63–74.

Burghardt, K. T., D. W. Tallamy, and W. Gregory Shriver (2009). Impact of Native Plants on Bird and Butterfly Biodiversity in Suburban Landscapes. Conservation Biology 23:219–224.

Burghardt, K. T., D. W. Tallamy, C. Philips, and K. J. Shropshire (2010). Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere 1:art11.

Burroughs, J. (1923). Bird Stories from Burroughs: Sketches of Bird Life Taken from the Works of John Burroughs. Houghton Mifflin.

Burt, C. S., J. F. Kelly, G. E. Trankina, C. L. Silva, A. Khalighifar, H. C. Jenkins-Smith, A. S. Fox, K. M. Fristrup, and K. G. Horton (2023). The effects of light pollution on migratory animal behavior. Trends in Ecology & Evolution. https://doi.org/10.1016/j.tree.2022.12.006

Buxton, R. T., M. F. McKenna, D. Mennitt, K. Fristrup, K. Crooks, L. Angeloni, and G. Wittemyer (2017). Noise pollution is pervasive in U.S. protected areas. Science 356:531–533.

Cabrera-Cruz, S. A., E. B. Cohen, J. A. Smolinsky, and J. J. Buler (2020). Artificial light at night is related to broad-scale stopover distributions of nocturnally migrating landbirds along the Yucatan Peninsula, Mexico. Remote Sensing 12:395.

Cabrera-Cruz, S. A., R. P. Larkin, M. E. Gimpel, J. G. Gruber, T. J. Zenzal Jr, and J. J. Buler (2021). Potential Effect of Low-Rise, Downcast Artificial Lights on Nocturnally Migrating Land Birds. Integrative and Comparative Biology 61:1216–1236.

Cabrera-Cruz, S. A., J. A. Smolinsky, and J. J. Buler (2018a). Light pollution is greatest within migration passage areas for nocturnally-migrating birds around the world. Scientific Reports 8:3261.

Cabrera-Cruz, S. A., J. A. Smolinsky, and J. J. Buler (2018b). Light pollution is greatest within migration passage areas for nocturnally-migrating birds around the world. Scientific Reports 8:3261.

Cabrera-Cruz, S. A., J. A. Smolinsky, K. P. McCarthy, and J. J. Buler (2019). Urban areas affect flight altitudes of nocturnally migrating birds. Journal of Animal Ecology 88:1873–1887.

Calvert, A., C. Bishop, R. Elliot, E. Krebs, T. Kydd, C. Machtans, and G. Robertson (2013a). A Synthesis of Human-related Avian Mortality in Canada. Avian Conservation and Ecology 8.

Calvert, A. M., C. A. Bishop, R. D. Elliot, E. A. Krebs, T. M. Kydd, C. S. Machtans, and G. J. Robertson (2013b). A Synthesis of Human-related Avian Mortality in Canada. Avian Conservation and Ecology 8:art11.

Calvert, A. M., S. J. Walde, and P. D. Taylor (2009). Nonbreeding-Season Drivers of Population Dynamics in Seasonal Migrants: Conservation Parallels Across Taxa. Avian Conservation and Ecology 4:art5.

Carey, C. (2009). The impacts of climate change on the annual cycles of birds. Philosophical Transactions of the Royal Society B: Biological Sciences 364:3321–3330.

Caro, T. (2005). Antipredator Defenses in Birds and Mammals. University of Chicago Press.

Castañeda, I., C. Bellard, I. Jarić, B. Pisanu, J.-L. Chapuis, and E. Bonnaud (2019). Trophic patterns and home-range size of two generalist urban carnivores: a review. Journal of Zoology 307:79–92.

Castro-Prieto, J., and M. J. Andrade-Núñez (2018). Health and Ecological Aspects of Stray Cats in Old San Juan, Puerto Rico: Baseline Information to Develop an Effective Control Program. Puerto Rico Health Sciences Journal 37:110–114.

Castro-Prieto, J., M. Quiniones, and W. Gould (2016). Characterization of the network of protected areas in Puerto Rico. Caribbean Naturalist:1–16.

Castro-Prieto, J., J. M. Wunderle, Jr., J. Salguero-Faría, S. Soto-Bayó, J. Crespo, and W. Gould (2021). Puerto Rico Breeding Bird Atlas.

Cayton, H. L., N. M. Haddad, K. Gross, S. E. Diamond, and L. Ries (2015). Do growing degree days predict phenology across butterfly species? Ecology 96:1473–1479.

Cerasale, D. J., and C. G. Guglielmo (2010). An Integrative Assessment of the Effects of Tamarisk on Stopover Ecology of a Long-Distance Migrant Along the San Pedro River, Arizona. The Auk 127:636–646.

Chalkowski, K., A. E. Wilson, C. A. Lepczyk, and S. Zohdy (2019). Who let the cats out? A global meta-analysis on risk of parasitic infection in indoor versus outdoor domestic cats ( *Felis catus* ). Biology Letters 15:20180840.

Charmantier, A., and P. Gienapp (2014). Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. Evolutionary Applications 7:15–28.

Chatham-Stephens, K., J. Caravanos, B. Ericson, J. Sunga-Amparo, B. Susilorini, P. Sharma, P. J. Landrigan, and R. Fuller (2013). Burden of disease from toxic waste sites in India, Indonesia, and the Philippines in 2010. Environmental health perspectives 121:791–796.

Cheng, S. J., K. M. Gaynor, A. C. Moore, K. Darragh, C. O. Estien, J. W. Hammond, C. Lawrence, K. L. Mills, M. D. Baiz, D. Ignace, L. Khadempour, et al. (2023).

Championing inclusive terminology in ecology and evolution. Trends in Ecology & Evolution. https://doi.org/10.1016/j.tree.2022.12.011

Chernetsov, N. (2006). Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147:185–191.

Cid, F. D., R. I. Antón, and E. Caviedes-Vidal (2007). Organochlorine pesticide contamination in three bird species of the Embalse La Florida water reservoir in the semiarid midwest of Argentina. Science of the Total Environment 385:86–96.

Cimprich, D. A., and F. R. Moore (2006). Fat affects predator-avoidance behavior in Gray Catbirds (Dumetella carolinensis) during migratory stopover. The Auk 123:9.

Cimprich, D. A., M. S. Woodrey, and F. R. Moore (2005a). Passerine migrants respond to variation in predation risk during stopover. Animal Behaviour 69:1173–1179.

Cimprich, D. A., M. S. Woodrey, and F. R. Moore (2005b). Passerine migrants respond to variation in predation risk during stopover. Animal Behaviour 69:1173–1179.

Clements, S. J., J. P. Loghry, B. M. Ballard, and M. D. Weegman (2022). Carry-over effects of weather and decision-making on nest success of a migratory shorebird. Ecology and Evolution 12:e9581.

Cochran, W. W., and C. J. Kjos (1985). Wind drift and migration of thrushes: a telemetry study. Illinois Natural History Survey Bulletin 33:297–330.

Cohen, E. B., W. C. Barrow, J. J. Buler, J. L. Deppe, A. Farnsworth, P. P. Marra, S. R. McWilliams, D. W. Mehlman, R. R. Wilson, M. S. Woodrey, and F. R. Moore (2017). How do en route events around the Gulf of Mexico influence migratory landbird populations? The Condor 119:327–343.

Cohen, E. B., J. J. Buler, K. G. Horton, S. R. Loss, S. A. Cabrera-Cruz, J. A. Smolinsky, and P. P. Marra (2022a). Using weather radar to help minimize wind energy impacts on nocturnally migrating birds. Conservation Letters n/a:e12887.

Cohen, E. B., K. G. Horton, P. P. Marra, H. L. Clipp, A. Farnsworth, J. A. Smolinsky, D. Sheldon, and J. J. Buler (2021). A place to land: spatiotemporal drivers of stopover habitat use by migrating birds. Ecology Letters 24:38–49.

Cohen, E. B., J. A. Hostetler, M. T. Hallworth, C. S. Rushing, T. S. Sillett, and P. P. Marra (2018). Quantifying the strength of migratory connectivity. Methods in Ecology and Evolution 9:513–524.

Cohen, E. B., J. M. Lafleur, and F. R. Moore (2022b). Density Dependent Refueling of Migratory Songbirds During Stopover Within an Urbanizing Coastal Landscape. Frontiers in Ecology and Evolution 10.

Cohen, E. B., F. R. Moore, and R. A. Fischer (2012). Experimental Evidence for the Interplay of Exogenous and Endogenous Factors on the Movement Ecology of a Migrating Songbird. PLoS ONE 7:e41818.

Cohen, E. B., Z. Németh, T. J. Zenzal, K. L. Paxton, R. H. Diehl, E. H. Paxton, and F. R. Moore (2015). Spring resource phenology and timing of songbird migration across the Gulf of Mexico. In Phenological Synchrony and Bird Migration (E. M. Wood and J. L. Kellermann, Editors). 0 edition. CRC Press, pp. 63–82.

Cohen, E. B., C. R. Rushing, F. R. Moore, M. T. Hallworth, J. A. Hostetler, M. Gutierrez Ramirez, and P. P. Marra (2019). The strength of migratory connectivity for birds en route to breeding through the Gulf of Mexico. Ecography 42:658–669.

Cohen, E. B., and D. A. Satterfield (2020). 'Chancing on a spectacle:' co-occurring animal migrations and interspecific interactions. Ecography 43:1657–1671.

Colabuono, F. I., S. Taniguchi, and R. C. Montone (2012). Organochlorine contaminants in albatrosses and petrels during migration in South Atlantic Ocean. Chemosphere 86:701–708.

Connare, B. M., and K. Islam (2022). Failure to advance migratory phenology in response to climate change may pose a significant threat to a declining Nearctic-Neotropical songbird. International Journal of Biometeorology. https://doi.org/10.1007/s00484-022-02239-9

Cooper, N. W., T. W. Sherry, and P. P. Marra (2015). Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology 96:1933–1942.

Cornelius, J. M., T. Boswell, S. Jenni-Eiermann, C. W. Breuner, and M. Ramenofsky (2013). Contributions of endocrinology to the migration life history of birds. General and Comparative Endocrinology 190:47–60.

Costa, J. S., S. Hahn, P. M. Araújo, K. L. Dhanjal-Adams, A. D. Rocha, and J. A. Alves (2021). Linking migratory performance to breeding phenology and productivity in an Afro-Palearctic long-distance migrant. Scientific Reports 11:23258.

Costantini, D., and A. P. Møller (2008). Carotenoids Are Minor Antioxidants for Birds. Functional Ecology 22:367–370.

Coues, E. (1876). The Destruction of Birds by Telegraph Wire. The American Naturalist 10:734–736.

Courchamp, F., J.-L. Chapuis, and M. Pascal (2003). Mammal invaders on islands: impact, control and control impact. Biological Reviews 78:347–383.

Courchamp, F., M. Langlais, and G. Sugihara (1999). Cats protecting birds: modelling the mesopredator release effect. Journal of Animal Ecology 68:282–292.

Cove, M. V., B. Gardner, T. R. Simons, R. Kays, and A. F. O'Connell (2018). Free-ranging domestic cats (Felis catus) on public lands: estimating density, activity, and diet in the Florida Keys. Biological Invasions 20:333–344.

Cove, M. V., V. Herrmann, D. J. Herrera, B. C. Augustine, D. T. T. Flockhart, and W. J. McShea (2023). Counting the Capital's cats: Estimating drivers of abundance of free-roaming cats with a novel hierarchical model. Ecological Applications 33:e2790.

Cove, M. V., R. Kays, H. Bontrager, C. Bresnan, M. Lasky, T. Frerichs, R. Klann, T. E. Lee Jr., S. C. Crockett, A. P. Crupi, K. C. B. Weiss, et al. (2021). SNAPSHOT USA 2019: a coordinated national camera trap survey of the United States. Ecology 102:e03353.

Cresswell, W. (2008a). Non-lethal effects of predation in birds: Non-lethal effects of predation risks. Ibis 150:3–17.

Cresswell, W. (2008b). Non-lethal effects of predation in birds: Non-lethal effects of predation risks. Ibis 150:3–17.

Cresswell, W. (2011). Predation in bird populations. Journal of Ornithology 152:251–263.

Crewe, T. L., Z. J. Crysler, and P. D. Taylor (2018). Motus R Book: a walk through the use of R for Motus automated radio-telemetry data. [Online.] Available at https://motus.org/MotusRBook/.

Crooks, K. R., and M. E. Soulé (1999). Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Crowley, S. L., S. Hinchliffe, and R. A. McDonald (2017). Conflict in invasive species management. Frontiers in Ecology and the Environment 15:133–141.

Cullen, A. C., K. E. Farley, S. S. Pagano, F. J. Gallagher, and C. Holzapfel (2020). All in the timing: how fruit nutritional content influences the timing of fruit consumption of two invasive shrubs. Plant Ecology 221:951–963.

Curley, S. R., L. L. Manne, and R. R. Veit (2020). Differential winter and breeding range shifts: Implications for avian migration distances. Diversity and Distributions 26:415–425.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, et al. (2001). Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51:723–734.

Darling, E. S., and I. M. Côté (2008). Quantifying the evidence for ecological synergies. Ecology Letters 11:1278–1286.

David A. Cimprich and Frank R. Moore (2006). FAT AFFECTS PREDATOR-AVOIDANCE BEHAVIOR IN GRAY CATBIRDS (DUMETELLA CAROLINENSIS) DURING MIGRATORY STOPOVER. 123:9.

Davis, K. (1955). The origin and growth of urbanization in the world. American Journal of Sociology 60:429–437.

Davy, C. M., A. T. Ford, and K. C. Fraser (2017). Aeroconservation for the Fragmented Skies. Conservation Letters 10:773–780.

Day, R. H., J. R. Rose, A. K. Prichard, and B. Streever (2015). Effects of Gas Flaring on the Behavior of Night-Migrating Birds at an Artificial Oil-Production Island, Arctic Alaska. Arctic 68:367–379.

Dayer, A. A., K. H. Redford, K. J. Campbell, C. R. Dickman, R. S. Epanchin-Niell, E. D. Grosholz, D. E. Hallac, E. F. Leslie, L. A. Richardson, and M. W. Schwartz (2020). The unaddressed threat of invasive animals in U.S. National Parks. Biological Invasions 22:177–188.

Deakin, J. E., C. G. Guglielmo, and Y. E. Morbey (2019). Sex differences in migratory restlessness behavior in a Nearctic–Neotropical songbird. The Auk 136:ukz017.

Deakin, J. E., C. G. Guglielmo, and Y. E. Morbey (2021). Effect of the Social Environment on Spring Migration Timing of a Songbird. Frontiers in Ecology and Evolution 9:715418.

DeCandido, R., and D. Allen (2006). Nocturnal hunting by Peregrine Falcons at the Empire State Building, New York City. The Wilson Journal of Ornithology 118:53–58.

Decker, D. J., A. B. Forstchen, W. F. Siemer, C. A. Smith, R. K. Frohlich, M. V. Schiavone, P. E. Lederle, and E. F. Pomeranz (2019). Moving the paradigm from stakeholders to beneficiaries in wildlife management. The Journal of Wildlife Management 83:513–518.

Demir, A., and K. G. Ozsemir (2021). Ocular Lesions and Neurologic Findings in Traumatic Birds: A Retrospective Evalution of 114 Cases. Erciyes Üniversitesi Veteriner Fakültesi Dergisi 18:19–25.

Des Roches, S., K. I. Brans, M. R. Lambert, L. R. Rivkin, A. M. Savage, C. J. Schell, C. Correa, L. De Meester, S. E. Diamond, N. B. Grimm, N. C. Harris, et al. (2021). Socio-eco-evolutionary dynamics in cities. Evolutionary Applications 14:248–267.

Dias, R. A., C. R. Abrahão, T. Micheletti, P. R. Mangini, V. P. de Oliveira Gasparotto, H. F. de Jesus Pena, F. Ferreira, J. C. Russell, and J. C. R. Silva (2017). Prospects for domestic and feral cat management on an inhabited tropical island. Biological Invasions 19:2339–2353.

Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand, and R. M. Ewers (2007). Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology & Evolution 22:489–496.

Dierschke, V. (2003a). Predation hazard during migratory stopover: are light or heavy birds under risk? Journal of Avian Biology 34:24–29.

Dierschke, V. (2003b). Predation hazard during migratory stopover: are light or heavy birds under risk? Journal of Avian Biology 34:24–29.

Doherty, T., W. Geary, C. Jolly, K. Macdonald, V. Miritis, D. Watchorn, M. Cherry, L. Conner, T. Gonzalez, S. Legge, E. Ritchie, et al. (2022). Fire as a driver and mediator of predator-prey interactions. Biological reviews of the Cambridge Philosophical Society 97.

Doherty, T. S., C. R. Dickman, D. G. Nimmo, and E. G. Ritchie (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. Biological Conservation 190:60–68.

Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman (2016a). Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences 113:11261–11265.

Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman (2016b). Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences 113:11261–11265.

Dokter, A. M., A. Farnsworth, D. Fink, V. Ruiz-Gutierrez, W. M. Hochachka, F. A. La Sorte, O. J. Robinson, K. V. Rosenberg, and S. Kelling (2018). Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. Nature Ecology & Evolution 2:1603–1609.

Dominoni, D. M., W. Goymann, B. Helm, and J. Partecke (2013a). Urban-like night illumination reduces melatonin release in European blackbirds (Turdus merula): implications of city life for biological time-keeping of songbirds. Frontiers in Zoology 10:1–11.

Dominoni, D., M. Quetting, and J. Partecke (2013b). Artificial light at night advances avian reproductive physiology. Proceedings of the Royal Society B: Biological Sciences 280:20123017.

Donnelly, A., R. Yu, A. Caffarra, J. Hanes, L. Liang, A. R. Desai, L. Liu, and M. D. Schwartz (2017). Interspecific and interannual variation in the duration of spring phenophases in a northern mixed forest. Agricultural and Forest Meteorology 243:55–67.

Dossman, B. C., A. D. Rodewald, C. E. Studds, and P. P. Marra (2022). Migratory birds with delayed spring departure migrate faster but pay the costs. Ecology n/a:e3938.

Drent, R. H., B. S. Ebbinge, and B. Weijand (1978). Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verhandl. Ornithol. Gesellschaft Bayern 23:239–264.

Drewitt, A. L., and R. H. W. Langston (2008). Collision effects of wind-power generators and other obstacles on birds. Annals of the New York Academy of Sciences 1134:233–266.

Driscoll, C. A., J. Clutton-Brock, A. C. Kitchener, and S. J. O'Brien (2009). The Taming of the Cat. Scientific American 300:68–75.

Duijns, S., J. G. B. van Dijk, B. Spaans, J. Jukema, W. F. D. Boer, and T. Piersma (2009). Foraging Site Selection of Two Subspecies of Bar-tailed Godwit Limosa lapponica: Time Minimizers Accept Greater Predation Danger Than Energy Minimizers. Ardea 97:51–59.

Dunn, E. H. (2016). Bird Observatories: An Underutilized Resource For Migration Study. The Wilson Journal of Ornithology 128:691–703.

Dutta, H. (2017). Insights into the impacts of four current environmental problems on flying birds. Energy, Ecology and Environment 2:329–349.

Dyer, E. E., P. Cassey, D. W. Redding, B. Collen, V. Franks, K. J. Gaston, K. E. Jones, S. Kark, C. D. L. Orme, and T. M. Blackburn (2017). The Global Distribution and Drivers of Alien Bird Species Richness. PLOS Biology 15:e2000942.

Edmonds, S. T., N. J. O'Driscoll, N. K. Hillier, J. L. Atwood, and D. C. Evers (2012). Factors regulating the bioavailability of methylmercury to breeding rusty blackbirds in northeastern wetlands. Environmental Pollution 171:148–154.

Efford, M. G., D. L. Borchers, and A. E. Byrom (2009). Density Estimation by Spatially Explicit Capture–Recapture: Likelihood-Based Methods. In Modeling Demographic Processes In Marked Populations (D. L. Thomson, E. G. Cooch and M. J. Conroy, Editors). Springer US, Boston, MA, pp. 255–269.

Efford, M. G., and G. Mowat (2014). Compensatory heterogeneity in spatially explicit capture–recapture data. Ecology 95:1341–1348.

Eikenaar, C., and J. L. Schläfke (2013). Size and accumulation of fuel reserves at stopover predict nocturnal restlessness in a migratory bird. Biology Letters 9:20130712.

Elizondo, E. C., and S. R. Loss (2016). Using trail cameras to estimate free-ranging domestic cat abundance in urban areas. Wildlife Biology 22:246–252.

Elliott, J. E., and C. A. Bishop (2011). 13 Cyclodiene and Other Organochlorine Pesticides in Birds. Environmental Contaminants in Biota: Interpreting Tissue Concentrations:447.

Elmore, A. J., S. M. Guinn, B. J. Minsley, and A. D. Richardson (2012). Landscape controls on the timing of spring, autumn, and growing season length in mid-Atlantic forests. Global Change Biology 18:656–674.

Elmore, A. J., C. Stylinski, and K. Pradhan (2016). Synergistic Use of Citizen Science and Remote Sensing for Continental-Scale Measurements of Forest Tree Phenology. Remote Sensing 8:502.

Eng, M. L., B. J. Stutchbury, and C. A. Morrissey (2017). Imidacloprid and chlorpyrifos insecticides impair migratory ability in a seed-eating songbird. Scientific reports 7:1–9.

Eng, M. L., B. J. Stutchbury, and C. A. Morrissey (2019). A neonicotinoid insecticide reduces fueling and delays migration in songbirds. Science 365:1177–1180.

Engeman, R. M., S. A. Shwiff, F. Cano, and B. Constantin (2003). An economic assessment of the potential for predator management to benefit Puerto Rican parrots. Ecological Economics 46:283–292.

Engeman, R., D. Whisson, J. Quinn, F. Cano, P. Quiñones, and T. H. White Jr (2006). Monitoring invasive mammalian predator populations sharing habitat with the Critically Endangered Puerto Rican parrot *Amazona vittata*. Oryx 40:95–102.

Engstrom, R. T. (2010). First-Order Fire Effects on Animals: Review and Recommendations. Fire Ecology 6:115–130.

Escobar-Ibáñez, J. F., R. Rueda-Hernández, and I. MacGregor-Fors (2020). The Greener the Better! Avian Communities Across a Neotropical Gradient of Urbanization Density. Frontiers in Ecology and Evolution 8.

Evans, W. R., Y. Akashi, N. S. Altman, and A. M. Manville (2007). Response of night-migrating songbirds in cloud to colored and flashing light. North American Birds 60:476–488.

Falcón, W., and R. L. Tremblay (2018). From the cage to the wild: introductions of Psittaciformes to Puerto Rico. PeerJ 6:e5669.

Fardell, L. L., C. R. Pavey, and C. R. Dickman (2023). Influences of roaming domestic cats on wildlife activity in patchy urban environments. Frontiers in Ecology and Evolution 11.

Fernández-Arellano, G. J., A. L. Teixido, B. Bernardon, E. R. Bueno, T. V. Ferreira, S. R. A. Gonçalves, M. Jesus, K. P. C. S. Thomas, M. Zucchetto, V. Q. Piacentini, and J. B. Pinho (2021). Knowledge gaps and biases in the Pantanal indicate future directions for ornithological research in large wetlands. Ibis 163:784–797.

Fernández-Juricic, E. (2012). Sensory basis of vigilance behavior in birds: Synthesis and future prospects. Behavioural Processes 89:143–152.

Finch, D. M., D. Pearson, J. Wunderle, and W. Arendt (2010). Terrestrial Animals as Invasive Species and as Species at Risk From Invasions. In A Dynamic Invasive Species Research Vision: Opportunities and Priorities 2009–29 (M. E. Dix and K. Britton, Editors). U.S. Department of Agriculture Forest Service.

Finch, T., J. W. Pearce-Higgins, D. I. Leech, and K. L. Evans (2014). Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. Biodiversity and Conservation 23:2427–2444.

Finkler, H., E. Hatna, and J. Terkel (2011). The influence of neighbourhood socio-demographic factors on densities of free-roaming cat populations in an urban ecosystem in Israel. Wildlife Research 38:235.

Fischer, R. A., J. J. Valente, and M. P. Guilfoyle (2015). SPRING MIGRANT USE OF NATIVE AND SALTCEDAR-DOMINATED RIPARIAN AREAS ALONG THE LOWER COLORADO RIVER IN ARIZONA. Southwestern Naturalist 60:6–14.

Flockhart, D. T. T., and J. B. Coe (2018). Multistate matrix population model to assess the contributions and impacts on population abundance of domestic cats in urban areas including owned cats, unowned cats, and cats in shelters. PLOS ONE 13:e0192139.

Flockhart, D. T. T., D. R. Norris, and J. B. Coe (2016a). Predicting free-roaming cat population densities in urban areas. Animal Conservation 19:472–483.

Flockhart, D. T. T., D. R. Norris, and J. B. Coe (2016b). Predicting free-roaming cat population densities in urban areas. Animal Conservation 19:472–483.

Fornazari, G. A., A. Saldanha, R. R. Lange, T. Froes, D. Klem, B. A. Moore, and F. Montiani-Ferreira (2021). Window Collisions by Birds in Brazil: Epidemiologic Factors and Radiographic and Necropsy Assessments. Journal of Avian Medicine and Surgery 35:313–324.

Francis, C., and J. Barber (2013). A framework for understanding noise impacts on wildlife: An urgent conservation priority. Frontiers in Ecology and the Environment 11.

Francis, C. D. (2015). Vocal traits and diet explain avian sensitivities to anthropogenic noise. Global Change Biology 21:1809–1820.

Fransson, T., and T. P. Weber (1997a). Migratory fuelling in blackcaps ( Sylvia atricapilla ) under perceived risk of predation. Behavioral Ecology and Sociobiology 41:75–80.

Fransson, T., and T. P. Weber (1997b). Migratory fuelling in blackcaps ( Sylvia atricapilla ) under perceived risk of predation. Behavioral Ecology and Sociobiology 41:75–80.

Fraser, K. C., K. T. A. Davies, C. M. Davy, A. T. Ford, D. T. T. Flockhart, and E. G. Martins (2018). Tracking the Conservation Promise of Movement Ecology. Frontiers in Ecology and Evolution 6:150.

Freeberg, T. M., D. L. Book, and R. L. Weiner (2016). Foraging and Calling Behavior of Carolina chickadees ( *Poecile carolinensis* ) in Response to the Head Orientation of Potential Predators. Ethology 122:10–19.

Friend, M., and D. O. Trainer (1974). Response of different-age mallards to DDT. Bulletin of Environmental Contamination and Toxicology 11:49–56.

Galindo, J. C., R. J. Kendall, C. J. Driver, and T. E. Lacher (1985). The effect of methyl parathion on susceptibility of bobwhite quail (Colinus virginianus) to domestic cat predation. Behavioral and Neural Biology 43:21–36.

Gallinat, A. S., R. B. Primack, and T. L. Lloyd-Evans (2020). Can invasive species replace native species as a resource for birds under climate change? A case study on bird-fruit interactions. Biological Conservation 241.

García, M. A., J. A. Cruz-Burgos, E. Ventosa-Febles, and R. López-Ortiz (2005a). PUERTO RICO COMPREHENSIVE WILDLIFE CONSERVATION STRATEGY. 178.

García, M. A., J. A. Cruz-Burgos, E. Ventosa-Febles, and R. López-Ortiz (2005b). Puerto Rico Comperehensive Wildlife Conservation Strategy. Departamento de Recursos Naturales y Ambientales.

Gaston, K. J., T. M. Blackburn, and K. K. Goldewijk (2003). Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:1293–1300.

Gauthreaux, S. A. (1982). Age-dependent orientation in migratory birds. In Avian navigation. International symposium on avian navigation (ISAN) held at Tirrenia (Pisa), September 11-14, 1981 (F. Papi and H. G. Wallraff, Editors). Springer, Berlin, pp. 68–74.

Gauthreaux, S. A., and C. G. Belser (2006). Effects of artificial night lighting on migrating birds. In Ecological consequences of artificial night lighting (C. Rich and T. Longcore, Editors). Island Press, Washington, D.C., pp. 67–93.

Gerhold, R. W., and D. A. Jessup (2013). Zoonotic Diseases Associated with Free-Roaming Cats: Zoonoses and Free-Roaming Cats. Zoonoses and Public Health 60:189–195.

Giza, C. C., and D. A. Hovda (2001). The neurometabolic cascade of concussion. Journal of Athletic Training 36:228–235.

Gómez, C., N. J. Bayly, D. R. Norris, S. A. Mackenzie, K. V. Rosenberg, P. D. Taylor, K. A. Hobson, and C. Daniel Cadena (2017). Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. Scientific Reports 7:3405.

Gómez, C., S. L. Guerrero, A. M. FitzGerald, N. J. Bayly, K. A. Hobson, and C. D. Cadena (2019). Range-wide populations of a long-distance migratory songbird converge during stopover in the tropics. Ecological Monographs 89:e01349.

Gómez-Martínez, M. A., D. Klem, O. Rojas-Soto, F. González-García, and I. MacGregor-Fors (2019). Window strikes: bird collisions in a Neotropical green city. Urban Ecosystems 22:699–708.

González, A. M., N. J. Bayly, and K. A. Hobson (2020). Earlier and slower or later and faster: Spring migration pace linked to departure time in a Neotropical migrant songbird. Journal of Animal Ecology 89:2840–2851.

González-Prieto, A. M., and K. A. Hobson (2013). Environmental conditions on wintering grounds and during migration influence spring nutritional condition and arrival

phenology of Neotropical migrants at a northern stopover site. Journal of Ornithology 154:1067–1078.

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. Climate Research 35:37–58.

Gottfried, B. M. (1979). Anti-Predator Aggression in Birds Nesting in Old Field Habitats: An Experimental Analysis. The Condor 81:251–257.

Goulson, D. (2013). An overview of the environmental risks posed by neonicotinoid insecticides. Journal of Applied Ecology 50:977–987.

Gow, E. A., J. B. Burant, A. O. Sutton, N. E. Freeman, E. R. M. Grahame, M. Fuirst, M. C. Sorensen, S. M. Knight, H. E. Clyde, N. J. Quarrell, A. A. E. Wilcox, et al. (2022). Popular press portrayal of issues surrounding free-roaming domestic cats Felis catus. People and Nature 4:143–154.

van der Graaf, S. A. J., J. Stahl, A. Klimkowska, J. P. Bakker, and R. H. Drent (2006). Surfing on a green wave - how plant growth drives spring migration in the Barnacle Goose Branta leucopsis. Ardea 94:567–577.

Grandmont, T., P. Fast, I. Grentzmann, G. Gauthier, J. Bêty, and P. Legagneux (2023). Should I breed or should I go? Manipulating individual state during migration influences breeding decisions in a long-lived bird species. Functional Ecology n/a.

Greenwell, C. N., M. C. Calver, and N. R. Loneragan (2019). Cat Gets Its Tern: A Case Study of Predation on a Threatened Coastal Seabird. Animals 9:445.

Grue, C. E. (1982). Response of common grackles to dietary concentrations of four organophosphate pesticides. Archives of Environmental Contamination and Toxicology 11:617–626.

Guglielmo, C. G., A. R. Gerson, E. R. Price, and Q. R. Hays (2017). The effects of dietary macronutrients on flight ability, energetics, and fuel metabolism of yellow-rumped warblers Setophaga coronata. Journal of Avian Biology 48:133–148.

Gunther, I., T. Raz, O. Berke, and E. Klement (2015). Nuisances and welfare of free-roaming cats in urban settings and their association with cat reproduction. Preventive Veterinary Medicine 119:203–210.

Guo, F., J. J. Buler, J. A. Smolinsky, and D. S. Wilcove (2023). Autumn stopover hotspots and multiscale habitat associations of migratory landbirds in the eastern United States. Proceedings of the National Academy of Sciences 120:e2203511120.

Gutierrez Ramirez, M., M. S. Griego, J. G. DeSimone, C. R. Elowe, and A. R. Gerson (2022). Depleted lean body mass after crossing an ecological barrier differentially affects stopover duration and refuelling rate among species of long-distance migratory birds. Functional Ecology 00:1–12.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. Journal of Experimental Biology 199:39–48.

Gylfe, Å., S. Bergström, J. Lundstróm, and B. Olsen (2000). Reactivation of Borrelia infection in birds. Nature 403:724–725.

Hager, S. B., B. J. Cosentino, M. A. Aguilar-Gómez, M. L. Anderson, M. Bakermans, T. J. Boves, D. Brandes, M. W. Butler, E. M. Butler, N. L. Cagle, R. Calderón-Parra, et al. (2017). Continent-wide analysis of how urbanization affects bird-window collision mortality in North America. Biological Conservation 212:209–215.

Haines-Young, R., and M. Potschin (2010). The links between biodiversity, ecosystem services and human well-being. In Ecosystem Ecology (D. G. Raffaelli and C. L. J. Frid, Editors). 1st edition. Cambridge University Press, pp. 110–139.

Hall, C. M., K. A. Bryant, K. Haskard, T. Major, S. Bruce, and M. C. Calver (2016). Factors determining the home ranges of pet cats: A meta-analysis. Biological Conservation 203:313–320.

Halupka, L., K. Wierucka, H. Sztwiertnia, and E. Klimczuk (2017). Conditions at autumn stopover sites affect survival of a migratory passerine. Journal of Ornithology 158:979–988.

Hamer, R. P., R. Z. Gardiner, K. M. Proft, C. N. Johnson, and M. E. Jones (2021). A triple threat: high population density, high foraging intensity and flexible habitat preferences explain high impact of feral cats on prey. Proceedings of the Royal Society B: Biological Sciences 288:20201194.

Hardesty-Moore, M., S. Deinet, R. Freeman, G. C. Titcomb, E. M. Dillon, K. Stears, M. Klope, A. Bui, D. Orr, H. S. Young, A. Miller-ter Kuile, et al. (2018). Migration in the Anthropocene: how collective navigation, environmental system and taxonomy shape the vulnerability of migratory species. Philosophical Transactions of the Royal Society B: Biological Sciences 373:20170017.

Harris, M. L., L. K. Wilson, J. E. Elliott, C. A. Bishop, A. D. Tomlin, and K. V. Henning (2000). Transfer of DDT and metabolites from fruit orchard soils to American robins (Turdus migratorius) twenty years after agricultural use of DDT in Canada. Archives of Environmental Contamination and Toxicology 39:205–220.

Havera, S. P., R. M. Whitton, and R. T. Shealy (1992). Blood Lead and Ingested and Embedded Shot in Diving Ducks during Spring. The Journal of Wildlife Management 56:539–545.

Hedenström, A. (2008). Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society B: Biological Sciences 363:287–299.

Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Heise, C. D., and F. R. Moore (2003). Age-Related Differences in Foraging Efficiency, Molt, and Fat Deposition of Gray Catbirds Prior to Autumn Migration. The Condor 105:496–504.

Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes (2008). Five Potential Consequences of Climate Change for Invasive Species. Conservation Biology 22:534–543.

Henderson, R. H. (1992). Consequences of predator introductions and habitat destruction on amphibians and reptiles in the post-Columbus West Indies. Caribbean Journal of Science 28:1–10.

Henkel, J. R., B. J. Sigel, and C. M. Taylor (2012). Large-Scale Impacts of the Deepwater Horizon Oil Spill: Can Local Disturbance Affect Distant Ecosystems through Migratory Shorebirds? BioScience 62:676–685.

Herrera, D. J., M. V. Cove, W. J. McShea, S. Decker, D. T. T. Flockhart, S. M. Moore, and T. Gallo (2022). Spatial and temporal overlap of domestic cats (Felis catus) and native urban wildlife. Frontiers in Ecology and Evolution 10.

Herrera, D. J., S. M. Moore, D. T. T. Flockhart, W. J. McShea, and M. V. Cove (2021). Thinking outside the park: recommendations for camera trapping mammal communities in the urban matrix. Journal of Urban Ecology 7:juaa036.

Herrera-Montes, M., and T. M. Aide (2011). Impacts of traffic noise on anuran and bird communities. Urban Ecosystems 14:415–427.

Hewson, C. M., K. Thorup, J. W. Pearce-Higgins, and P. W. Atkinson (2016). Population decline is linked to migration route in the Common Cuckoo. Nature Communications 7:12296.

Hladik, M. L., S. R. Corsi, D. W. Kolpin, A. K. Baldwin, B. R. Blackwell, and J. E. Cavallin (2018). Year-round presence of neonicotinoid insecticides in tributaries to the Great Lakes, USA. Environmental pollution 235:1022–1029.

Hobson, K. A., S. L. Van Wilgenburg, J. Faaborg, J. D. Toms, C. Rengifo, A. L. Sosa, Y. Aubry, and R. Brito Aguilar (2014). Connecting breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopes: a call for an isotopic atlas of migratory connectivity: Isotopic Atlas of Connectivity. Journal of Field Ornithology 85:237–257.

Hoffman, K. M., E. L. Davis, S. B. Wickham, K. Schang, A. Johnson, T. Larking, P. N. Lauriault, N. Quynh Le, E. Swerdfager, and A. J. Trant (2021). Conservation of Earth's biodiversity is embedded in Indigenous fire stewardship. Proceedings of the National Academy of Sciences 118:e2105073118.

Holcomb, S. R., A. A. Bass, C. S. Reid, M. A. Seymour, N. F. Lorenz, B. B. Gregory, S. M. Javed, and K. F. Balkum (2015). Louisiana Wildlife Action Plan. Louisiana Department of Wildlife and Fisheries.

Hope, D. D., D. B. Lank, and R. C. Ydenberg (2014). Mortality-minimizing sandpipers vary stopover behavior dependent on age and geographic proximity to migrating predators. Behavioral Ecology and Sociobiology 68:827–838.

Horton, K. G., F. A. La Sorte, D. Sheldon, T.-Y. Lin, K. Winner, G. Bernstein, S. Maji, W. M. Hochachka, and A. Farnsworth (2020). Phenology of nocturnal avian migration has shifted at the continental scale. Nature Climate Change 10:63–68.

Horton, K. G., S. R. Morris, B. M. Van Doren, and K. M. Covino (2023). Six decades of North American bird banding records reveal plasticity in migration phenology. Journal of Animal Ecology 00:1–13.

Horton, K. G., C. Nilsson, B. M. Van Doren, F. A. La Sorte, A. M. Dokter, and A. Farnsworth (2019a). Bright lights in the big cities: migratory birds' exposure to artificial light. Frontiers in Ecology and the Environment 17:209–214.

Horton, K. G., B. M. Van Doren, F. A. La Sorte, E. B. Cohen, H. L. Clipp, J. J. Buler, D. Fink, J. F. Kelly, and A. Farnsworth (2019b). Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico. Global Change Biology 25:1106–1118.

Hostetler, J. A., T. S. Sillett, and P. P. Marra (2015). Full-annual-cycle population models for migratory birds. The Auk 132:433–449.

Howard, C., P. A. Stephens, J. A. Tobias, C. Sheard, S. H. M. Butchart, and S. G. Willis (2018). Flight range, fuel load and the impact of climate change on the journeys of migrant birds. Proceedings of the Royal Society B: Biological Sciences 285:20172329.

Huang, Z., H. Li, Y. Wei, J. Xiong, and J. You (2020). Distribution and ecological risk of neonicotinoid insecticides in sediment in South China: Impact of regional characteristics and chemical properties. Science of the Total Environment 714:136878.

Hudecki, J., and E. Finegan (2018). Songbird collision injuries during migration season. Journal of Wildlife Rehabilitation 38:7–11.

Huntley, B., Y. C. Collingham, R. E. Green, G. M. Hilton, C. Rahbek, and S. G. Willis (2006). Potential impacts of climatic change upon geographical distributions of birds. Ibis 148:8–28.

Hurlbert, A. H., and Z. Liang (2012). Spatiotemporal Variation in Avian Migration Phenology: Citizen Science Reveals Effects of Climate Change. PLoS ONE 7:e31662.

Hwang, J., N. L. Gottdenker, D.-H. Oh, H.-W. Nam, H. Lee, and M.-S. Chun (2018). Disentangling the link between supplemental feeding, population density, and the prevalence of pathogens in urban stray cats. PeerJ 6:e4988.

Isbell, F., P. Balvanera, A. S. Mori, J.-S. He, J. M. Bullock, G. R. Regmi, E. W. Seabloom, S. Ferrier, O. E. Sala, N. R. Guerrero-Ramírez, J. Tavella, et al. (2022). Expert perspectives

on global biodiversity loss and its drivers and impacts on people. Frontiers in Ecology and the Environment n/a.

Iwaniuk, A. N., D. T. Koperski, K. M. Cheng, J. E. Elliott, L. K. Smith, L. K. Wilson, and D. R. W. Wylie (2006). The effects of environmental exposure to DDT on the brain of a songbird: Changes in structures associated with mating and song. Behavioural Brain Research 173:1–10.

Izawa, M., T. Doi, and Y. Ono (1991). Notes on the Spacing Pattern of the Feral Cats at High Density. Bull. Kitakyushu Mus. Nat. Hist. 10:109–113.

Jaga, K., and C. Dharmani (2003). Dharmani C. Global surveillance of DDT and DDE levels in human tissues. Int J Occup Med Environ Health:7–20.

Jenni, L., and M. Schaub (2003a). Behavioural and Physiological Reactions to Environmental Variation in Bird Migration: a Review. In Avian Migration (P. Berthold, E. Gwinner and E. Sonnenschein, Editors). Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 155–171.

Jenni, L., and M. Schaub (2003b). Behavioural and Physiological Reactions to Environmental Variation in Bird Migration: a Review. In Avian Migration (P. Berthold, E. Gwinner and E. Sonnenschein, Editors). Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 155–171.

Jeschke, P., R. Nauen, M. Schindler, and A. Elbert (2011). Overview of the Status and Global Strategy for Neonicotinoids. Journal of Agricultural and Food Chemistry 59:2897–2908.

Jolly, C. J., C. R. Dickman, T. S. Doherty, L. M. van Eeden, W. L. Geary, S. M. Legge, J. C. Z. Woinarski, and D. G. Nimmo (2022). Animal mortality during fire. Global Change Biology 28:2053–2065.

Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman (2015). Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6:7537.

Kammon, A. (2012). Ameliorating Effects of Vitamin E and Selenium on Immunological Alterations Induced by Imidacloprid Chronic Toxicity in Chickens. Journal of Environmental & Analytical Toxicology s4.

Karanth, K. U. (1995). Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. Biological Conservation 71:333–338.

Karanth, K. U., and J. D. Nichols (1998). Estimation of Tiger Densities in India Using Photographic Captures and Recaptures. Ecology 79:2852–2862.

Kark, S., A. Tulloch, A. Gordon, T. Mazor, N. Bunnefeld, and N. Levin (2015). Cross-boundary collaboration: key to the conservation puzzle. Current Opinion in Environmental Sustainability 12:12–24.

Katzner, T. E., M. A. Braham, T. J. Conkling, J. E. Diffendorfer, A. E. Duerr, S. R. Loss, D. M. Nelson, H. B. Vander Zanden, and J. L. Yee (2020). Assessing population-level consequences of anthropogenic stressors for terrestrial wildlife. Ecosphere 11:e03046.

Kays, R., R. R. Dunn, A. W. Parsons, B. Mcdonald, T. Perkins, S. A. Powers, L. Shell, J. L. McDonald, H. Cole, H. Kikillus, L. Woods, et al. (2020). The small home ranges and large local ecological impacts of pet cats. Animal Conservation 23:516–523.

Kellermann, J. L., and C. van Riper (2015). Detecting mismatches of bird migration stopover and tree phenology in response to changing climate. Oecologia 178:1227–1238.

Kelly, J. F., K. G. Horton, P. M. Stepanian, K. M. Beurs, T. Fagin, E. S. Bridge, and P. B. Chilson (2016). Novel measures of continental-scale avian migration phenology related to proximate environmental cues. Ecosphere 7.

Kenny, D., Y.-J. Kim, H. Lee, and R. Reading (2015). Blood lead levels for Eurasian black vultures (Aegypius monachus) migrating between Mongolia and the Republic of Korea. Journal of Asia-Pacific Biodiversity 8:199–202.

Kesic, R., J. E. Elliott, K. M. Fremlin, L. Gauthier, K. G. Drouillard, and C. A. Bishop (2021). Continuing Persistence and Biomagnification of DDT and Metabolites in Northern Temperate Fruit Orchard Avian Food Chains. Environmental Toxicology and Chemistry 40:3379–3391.

Kharouba, H. M., J. Ehrlén, A. Gelman, K. Bolmgren, J. M. Allen, S. E. Travers, and E. M. Wolkovich (2018). Global shifts in the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy of Sciences 115:5211–5216.

Khelifa, R., R. Zebsa, H. Amari, M. K. Mellal, S. Bensouilah, A. Laouar, and H. Mahdjoub (2017). Unravelling the drastic range retraction of an emblematic songbird of North Africa: potential threats to Afro-Palearctic migratory birds. Scientific Reports 7:1092.

Kimmel, K., M. Clark, and D. Tilman (2022). Impact of multiple small and persistent threats on extinction risk. Conservation Biology n/a.

Kirby, J. S., A. J. Stattersfield, S. H. M. Butchart, M. I. Evans, R. F. A. Grimmett, V. R. Jones, J. O'Sullivan, G. M. Tucker, and I. Newton (2008). Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conservation International 18:S49–S73.

Kittelberger, K., M. Miller, and Ç. Şekercioğlu (2022). Fall bird migration in western North America during a period of heightened wildfire activity. Avian Conservation and Ecology 17.

Klaassen, M., B. J. Hoye, B. A. Nolet, and W. A. Buttemer (2012). Ecophysiology of avian migration in the face of current global hazards. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1719–1732.

Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K.-M. Exo, F. Bairlein, and T. Alerstam (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83:176–184.

Klem, D. (1990). Bird Injuries, Cause of Death, and Recuperation from Collisions with Windows (Heridas, Causas de Muerte y Restablecimiento de Aves que Chocan con Ventanas). Journal of Field Ornithology 61:115–119.

van Kleunen, M., W. Dawson, F. Essl, J. Pergl, M. Winter, E. Weber, H. Kreft, P. Weigelt, J. Kartesz, M. Nishino, L. A. Antonova, et al. (2015). Global exchange and accumulation of non-native plants. Nature 525:100-+.

Knudsen, E., A. Lindén, C. Both, N. Jonzén, F. Pulido, N. Saino, W. J. Sutherland, L. A. Bach, T. Coppack, T. Ergon, P. Gienapp, et al. (2011). Challenging claims in the study of migratory birds and climate change. Biological Reviews 86:928–946.

Kobori, H., T. Kamamoto, H. Nomura, K. Oka, and R. Primack (2012). The effects of climate change on the phenology of winter birds in Yokohama, Japan. Ecological Research 27:173–180.

Kokko, H. (1999). Competition for early arrival in migratory birds. Journal of Animal Ecology 68:940–950.

Kölzsch, A., S. Bauer, R. de Boer, L. Griffin, D. Cabot, K.-M. Exo, H. P. van der Jeugd, and B. A. Nolet (2015). Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. Journal of Animal Ecology 84:272–283.

Korpach, A. M., C. J. Garroway, A. M. Mills, V. von Zuben, C. M. Davy, and K. C. Fraser (2022). Urbanization and artificial light at night reduce the functional connectivity of migratory aerial habitat. Ecography n/a:e05581.

Kraus, F. (2015). Impacts from Invasive Reptiles and Amphibians. Annual Review of Ecology, Evolution, and Systematics 46:75–97.

Krawchuk, M. A., M. A. Moritz, M.-A. Parisien, J. Van Dorn, and K. Hayhoe (2009). Global Pyrogeography: the Current and Future Distribution of Wildfire. PLoS ONE 4:e5102.

Kubelka, V., B. K. Sandercock, T. Székely, and R. P. Freckleton (2022). Animal migration to northern latitudes: environmental changes and increasing threats. Trends in Ecology & Evolution 37:30–41.

Kullberg, C., T. Fransson, and S. Jakobsson (1996). Impaired predator evasion in fat blackcaps (Sylvia atricapilla). Proceedings of the Royal Society of London. Series B: Biological Sciences 263:1671–1675.

Kullberg, C., S. Jakobsson, and T. Fransson (2000). High Migratory Fuel Loads Impair Predator Evasion in Sedge Warblers. The Auk 117:1034–1038.

Kummer, J. A., E. M. Bayne, and C. S. Machtans (2016). Use of citizen science to identify factors affecting bird–window collision risk at houses. The Condor 118:624–639.

Kummer, J., and E. Bayne (2015). Bird feeders and their effects on bird-window collisions at residential houses. Avian Conservation and Ecology 10.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen (2017). lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26.

La Sorte, F. A., M. F. J. Aronson, C. A. Lepczyk, and K. G. Horton (2022). Assessing the combined threats of artificial light at night and air pollution for the world's nocturnally migrating birds. Global Ecology and Biogeography 31:912–924.

La Sorte, F. A., and C. H. Graham (2021). Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds. Journal of Animal Ecology 90:343–355.

Lambertucci, S. A., E. L. C. Shepard, and R. P. Wilson (2015). Human-wildlife conflicts in a crowded airspace. Science 348:502–504.

Langin, K. M., P. P. Marra, Z. Németh, F. R. Moore, T. Kurt Kyser, and L. M. Ratcliffe (2009). Breeding latitude and timing of spring migration in songbirds crossing the Gulf of Mexico. Journal of Avian Biology 40:309–316.

Langner, H. W., R. Domenech, V. A. Slabe, and S. P. Sullivan (2015). Lead and Mercury in Fall Migrant Golden Eagles from Western North America. Archives of Environmental Contamination and Toxicology 69:54–61.

Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg (2003). Effects of predation danger on migration strategies of sandpipers. Oikos 103:303–319.

Lank, D. B., and R. C. Ydenberg (2003). Death and danger at migratory stopovers: problems with "predation risk." Journal of Avian Biology 34:225–228.

Larison, J. R., G. E. Likens, J. W. Fitzpatrick, and J. G. Crock (2000). Cadmium toxicity among wildlife in the Colorado Rocky Mountains. Nature 406:181–183.

Lasky, M., A. Parsons, S. Schuttler, A. Mash, L. Larson, B. Norton, B. Pease, H. Boone, L. Gatens, and R. Kays (2021). Candid Critters: Challenges and Solutions in a Large-Scale Citizen Science Camera Trap Project. Citizen Science: Theory and Practice 6:4.

Le Corre, N., G. Gélinaud, and L. Brigand (2009). Bird disturbance on conservation sites in Brittany (France): the standpoint of geographers. Journal of Coastal Conservation 13:109–118.

Lee, S., and D. K. Lee (2018). What is the proper way to apply the multiple comparison test? Korean Journal of Anesthesiology 71:353–360.

Lees, A. C., L. Haskell, T. Allinson, S. B. Bezeng, I. J. Burfield, L. M. Renjifo, K. V. Rosenberg, A. Viswanathan, and S. H. M. Butchart (2022). State of the World's Birds. Annual Review of Environment and Resources 47:6.1-6.30.

Legagneux, P., P. L. F. Fast, G. Gauthier, and J. Bêty (2012). Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proceedings of the Royal Society B: Biological Sciences 279:876–883.

Legge, S., B. P. Murphy, H. McGregor, J. C. Z. Woinarski, J. Augusteyn, G. Ballard, M. Baseler, T. Buckmaster, C. R. Dickman, T. Doherty, G. Edwards, et al. (2017). Enumerating a continental-scale threat: How many feral cats are in Australia? Biological Conservation 206:293–303.

Lei, J., Y. Jia, A. Zuo, Q. Zeng, L. Shi, Y. Zhou, H. Zhang, C. Lu, G. Lei, and L. Wen (2019). Bird Satellite Tracking Revealed Critical Protection Gaps in East Asian–Australasian Flyway. International Journal of Environmental Research and Public Health 16:1147.

Lenth, R. V. (2022). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.4-1. [Online.] Available at https://CRAN.R-project.org/package=emmeans.

Lenzner, B., G. Latombe, A. Schertler, H. Seebens, Q. Yang, M. Winter, P. Weigelt, M. van Kleunen, P. Pyšek, J. Pergl, H. Kreft, et al. (2022). Naturalized alien floras still carry the legacy of European colonialism. Nature Ecology & Evolution 6:1723–1732.

Lepczyk, C. A., D. C. Duffy, D. M. Bird, M. Calver, D. Cherkassky, L. Cherkassky, C. R. Dickman, D. Hunter, D. Jessup, T. Longcore, S. R. Loss, et al. (2022). A science-based policy for managing free-roaming cats. Biological Invasions. https://doi.org/10.1007/s10530-022-02888-2

Lepczyk, C. A., A. G. Mertig, and J. Liu (2004). Landowners and cat predation across rural-to-urban landscapes. Biological Conservation 115:191–201.

Li, Y., Y. Wan, H. Shen, S. R. Loss, P. P. Marra, and Z. Li (2021). Estimates of wildlife killed by free-ranging cats in China. Biological Conservation 253:108929.

Liang, Y., I. Rudik, E. Y. Zou, A. Johnston, A. D. Rodewald, and C. L. Kling (2020). Conservation cobenefits from air pollution regulation: Evidence from birds. Proceedings of the National Academy of Sciences 117:30900–30906.

Lima, S. L. (1998). Nonlethal Effects in the Ecology of Predator-Prey Interactions. BioScience 48:25–34.

Lima, S. L., and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lincoln, F. C. (1931). Some causes of mortality among birds. The Auk 48:538–546.

Lind, J., and W. Cresswell (2006a). Anti-predation behaviour during bird migration; the benefit of studying multiple behavioural dimensions. Journal of Ornithology 147:310–316.

Lind, J., and W. Cresswell (2006b). Anti-predation behaviour during bird migration; the benefit of studying multiple behavioural dimensions. Journal of Ornithology 147:310–316.

Lind, J., T. Fransson, S. Jakobsson, and C. Kullberg (1999). Reduced take-off ability in robins (Erithacus rubecula) due to migratory fuel load. Behavioral Ecology and Sociobiology 46:65–70.

Lindström, Å. (1989a). Finch Flock Size and Risk of Hawk Predation at a Migratory Stopover Site. The Auk 106:225–232.

Lindström, Å. (1989b). Finch Flock Size and Risk of Hawk Predation at a Migratory Stopover Site. The Auk 106:225–232.

Lindström, Å. (1990). The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. Behavioral Ecology 1:102–106.

Lindstrom, Å. (1990). The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. Behavioral Ecology 1:102–106.

Linscott, J. A., and N. R. Senner (2021). Beyond refueling: Investigating the diversity of functions of migratory stopover events. Ornithological Applications 123:duaa074.

Litt-Jukes, J. E. (2023). Migration in the Spotlight: A Comparative Investigation of Behavioural and Energetic Responses to Artificial Light at Night in Nocturnal Migrant and Nonmigrant Songbirds. [Online.] Available at https://harvest.usask.ca/handle/10388/14474.

Liu, J. A., O. H. Meléndez-Fernández, J. R. Bumgarner, and R. J. Nelson (2022). Effects of light pollution on photoperiod-driven seasonality. Hormones and Behavior 141:105150.

Liu, L., and X. Zhang (2020). Effects of temperature variability and extremes on spring phenology across the contiguous United States from 1982 to 2016. Scientific Reports 10:17952.

Longcore, T., and P. A. Smith (2013). On Avian Mortality Associated with Human Activities. Avian Conservation and Ecology 8:art1.

Lopez-Antia, A., M. E. Ortiz-Santaliestra, F. Mougeot, and R. Mateo (2013). Experimental exposure of red-legged partridges (Alectoris rufa) to seeds coated with imidacloprid, thiram and difenoconazole. Ecotoxicology 22:125–138.

Lopez-Antia, A., M. E. Ortiz-Santaliestra, F. Mougeot, and R. Mateo (2015). Imidacloprid-treated seed ingestion has lethal effect on adult partridges and reduces both breeding investment and offspring immunity. Environmental Research 136:97–107.

López-Ortiz, R., E. A. Ventosa-Febles, L. R. Reitsma, D. Hengstenberg, and W. Deluca (2002). Increasing nest success in the yellow-shouldered blackbird Agelaius xanthomus in southwest Puerto Rico. Biological Conservation 108:259–263.

Loss, S. R., B. Boughton, S. M. Cady, D. W. Londe, C. McKinney, T. J. O'Connell, G. J. Riggs, and E. P. Robertson (2022). Review and synthesis of the global literature on domestic cat impacts on wildlife. Journal of Animal Ecology 91:1361–1372.

Loss, S. R., and P. P. Marra (2017a). Population impacts of free-ranging domestic cats on mainland vertebrates. Frontiers in Ecology and the Environment 15:502–509.

Loss, S. R., and P. P. Marra (2017b). Population impacts of free-ranging domestic cats on mainland vertebrates. Frontiers in Ecology and the Environment 15:502–509.

Loss, S. R., and P. P. Marra (2018). Merchants of doubt in the free-ranging cat conflict. Conservation Biology 32:265–266.

Loss, S. R., T. Will, and P. P. Marra (2012). Direct human-caused mortality of birds: improving quantification of magnitude and assessment of population impact. Frontiers in Ecology and the Environment 10:357–364.

Loss, S. R., T. Will, and P. P. Marra (2013a). The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:1396.

Loss, S. R., T. Will, and P. P. Marra (2013b). The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:1396.

Loss, S. R., T. Will, and P. P. Marra (2015a). Direct Mortality of Birds from Anthropogenic Causes. Annual Review of Ecology, Evolution, and Systematics 46:99–120.

Loss, S. R., T. Will, and P. P. Marra (2015b). Direct mortality of birds from anthropogenic causes. Annual Review of Ecology, Evolution, and Systematics 46:99–120.

Loss, S. R., T. Will, and P. P. Marra (2015c). Direct Mortality of Birds from Anthropogenic Causes. Annual Review of Ecology, Evolution, and Systematics 46:99–120.

Lüdecke, D. (2018). ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. Journal of Open Source Software 3.

Lüdecke, D. (2022). sjPlot: Data Visualization for Statistics in Social Science. [Online.] Available at https://CRAN.R-project.org/package=sjPlot.

Lüdecke, D., M. S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software 6(60).

Ma, Y., B. A. Branfireun, K. A. Hobson, and C. G. Guglielmo (2018). Evidence of negative seasonal carry-over effects of breeding ground mercury exposure on survival of migratory songbirds. Journal of Avian Biology 49:jav-01656.

Ma, Y., C.-Y. Choi, A. Thomas, and L. Gibson (2022). Review of contaminant levels and effects in shorebirds: Knowledge gaps and conservation priorities. Ecotoxicology and Environmental Safety 242:113868.

Maas, B., R. J. Pakeman, L. Godet, L. Smith, V. Devictor, and R. Primack (2021). Women and Global South strikingly underrepresented among top-publishing ecologists. Conservation Letters 14:e12797.

MacGregor-Fors, I., F. Escobar, R. Rueda-Hernández, S. Avendaño-Reyes, M. L. Baena, V. M. Bandala, S. Chacón-Zapata, A. Guillén-Servent, F. González-García, F. Lorea-Hernández, E. Montes de Oca, et al. (2016). City "Green" Contributions: The Role of Urban Greenspaces as Reservoirs for Biodiversity. Forests 7:146.

MacGregor-Fors, I., L. Morales-Pérez, and J. E. Schondube (2010). Migrating to the City: Responses of Neotropical Migrant Bird Communities to Urbanization. The Condor 112:711–717.

MacGregor-Fors, I., C. C. Rega-Brodsky, M. García-Arroyo, M. A. Gómez-Martínez, and L.-B. Vázquez (2020). Urban bird ecologists cite more publications from the Global North; why? Journal of Urban Ecology 6:juaa027.

Mack, D. E., and W. Yong (2020). Swainson's Thrush (Catharus ustulatus), version 1.0. Birds of the World. https://doi.org/10.2173/bow.swathr.01

Maeda, T., R. Nakashita, K. Shionosaki, F. Yamada, and Y. Watari (2019). Predation on endangered species by human-subsidized domestic cats on Tokunoshima Island. Scientific Reports 9:16200.

Mahon, C. L., G. L. Holloway, E. M. Bayne, and J. D. Toms (2019). Additive and interactive cumulative effects on boreal landbirds: winners and losers in a multi-stressor landscape. Ecological Applications 29:e01895.

Maldonado, A. R., M. A. Mora, and J. L. Sericano (2017). Seasonal Differences in Contaminant Accumulation in Neotropical Migrant and Resident Songbirds. Archives of Environmental Contamination and Toxicology 72:39–49.

Mancuso, K. A., M. A. Fylling, C. A. Bishop, K. E. Hodges, M. B. Lancaster, and K. R. Stone (2021). Migration ecology of western gray catbirds. Movement Ecology 9:10.

Mansouri, I., M. Dakki, W. Squalli, H. Achiban, M. Mounir, and L. El Ghadraoui (2022). Wildlife-vehicle collisions in Moroccan Atlantic Sahara: Impact on resident species and Afro-Palearctic birds for conservation purposes. African Journal of Ecology. https://doi.org/10.1111/aje.13007

Marcacci, G., M. Briedis, N. Diop, A. Y. Diallo, F. Kebede, and A. Jacot (2022). A roadmap integrating research, policy, and actions to conserve Afro-Palearctic migratory landbirds at a flyway scale. Conservation Letters n/a:e12933.

Marques, A. T., H. Batalha, S. Rodrigues, H. Costa, M. J. R. Pereira, C. Fonseca, M. Mascarenhas, and J. Bernardino (2014). Understanding bird collisions at wind farms: An updated review on the causes and possible mitigation strategies. Biological Conservation 179:40–52.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

Marra, P. P., E. Cohen, A.-L. Harrison, C. E. Studds, and M. Webster (2019). Migratory Connectivity. In Encyclopedia of Animal Behavior (J. Choe, Editor). Oxford Academic Press, Oxford, UK, pp. 643–654.

Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore (2005). The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307–315.

Martinuzzi, S., A. J. Allstadt, B. L. Bateman, P. J. Heglund, A. M. Pidgeon, W. E. Thogmartin, S. J. Vavrus, and V. C. Radeloff (2016). Future frequencies of extreme weather events in the National Wildlife Refuges of the conterminous U.S. Biological Conservation 201:327–335.

Martinuzzi, S., W. A. Gould, and O. M. Ramos González (2007). Land development, land use, and urban sprawl in Puerto Rico integrating remote sensing and population census data. Landscape and Urban Planning 79:288–297.

Martinuzzi, S., O. M. Ramos-González, T. A. Muñoz-Erickson, D. H. Locke, A. E. Lugo, and V. C. Radeloff (2018). Vegetation cover in relation to socioeconomic factors in a tropical city assessed from sub-meter resolution imagery. Ecological Applications 28:681–693.

Mason, R., H. Tennekes, F. Sánchez-Bayo, and P. U. Jepsen (2013). Immune Suppression by Neonicotinoid Insecticides at the Root of Global Wildlife Declines. Journal of Enviromental Immunology and Toxicology 1:3.

Matthews, S. N., and P. G. Rodewald (2010). Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology 25:955–965.

Mayor, S. J., R. P. Guralnick, M. W. Tingley, J. Otegui, J. C. Withey, S. C. Elmendorf, M. E. Andrew, S. Leyk, I. S. Pearse, and D. C. Schneider (2017). Increasing phenological

asynchrony between spring green-up and arrival of migratory birds. Scientific Reports 7:1902.

McCabe, J. D., and B. J. Olsen (2015). Tradeoffs between predation risk and fruit resources shape habitat use of landbirds during autumn migration. The Auk 132:903–913.

McClure, C. J. W., H. E. Ware, J. D. Carlisle, and J. R. Barber (2017). Noise from a phantom road experiment alters the age structure of a community of migrating birds. Animal Conservation 20:164–172.

McClure, C. J. W., H. E. Ware, J. Carlisle, G. Kaltenecker, and J. R. Barber (2013). An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proceedings of the Royal Society B: Biological Sciences 280:20132290.

McCrory, P., W. Meeuwisse, J. Dvorak, M. Aubry, J. Bailes, S. Broglio, R. C. Cantu, D. Cassidy, R. J. Echemendia, R. J. Castellani, G. A. Davis, et al. (2017). Consensus statement on concussion in sport-the 5th international conference on concussion in sport held in Berlin, October 2016. British Journal of Sports Medicine 51:838–847.

McDermott, M. E., and L. W. DeGroote (2017). Linking phenological events in migratory passerines with a changing climate: 50 years in the Laurel Highlands of Pennsylvania. PLOS ONE 12:e0174247.

McDonald, J. L., and E. Skillings (2021). Human influences shape the first spatially explicit national estimate of urban unowned cat abundance. Scientific Reports 11:20216.

McKee, J., P. Shaw, A. Dekker, and K. Patrick (2016). Approaches to Wildlife Management in Aviation. In Problematic Wildlife: A Cross-Disciplinary Approach (F. M. Angelici, Editor). Springer International Publishing, Cham, pp. 465–488.

McKinney, M. L. (2004). Measuring floristic homogenization by non-native plants in North America. Global Ecology and Biogeography 13:47–53.

McKinnon, E. A., and O. P. Love (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. The Auk 135:834–856.

McLaren, J. D., J. J. Buler, T. Schreckengost, J. A. Smolinsky, M. Boone, E. Emiel van Loon, D. K. Dawson, and E. L. Walters (2018). Artificial light at night confounds broad-scale habitat use by migrating birds. Ecology Letters 21:356–364.

McLauchlan, K. K., P. E. Higuera, J. Miesel, B. M. Rogers, J. Schweitzer, J. K. Shuman, A. J. Tepley, J. M. Varner, T. T. Veblen, S. A. Adalsteinsson, J. K. Balch, et al. (2020). Fire as a fundamental ecological process: Research advances and frontiers. Journal of Ecology 108:2047–2069.

McWilliams, S., W. Carter, C. Cooper-Mullin, K. DeMoranville, A. Frawley, B. Pierce, and M. Skrip (2021). How Birds During Migration Maintain (Oxidative) Balance. Frontiers in Ecology and Evolution 9.

McWilliams, S. R., C. Guglielmo, B. Pierce, and M. Klaassen (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. Journal of Avian Biology 35:377–393.

Medina, F. M., E. Bonnaud, E. Vidal, and M. Nogales (2014). Underlying impacts of invasive cats on islands: not only a question of predation. Biodiversity and Conservation 23:327–342.

Medina, F. M., E. Bonnaud, E. Vidal, B. R. Tershy, E. S. Zavaleta, C. Josh Donlan, B. S. Keitt, M. Corre, S. V. Horwath, and M. Nogales (2011). A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17:3503–3510.

Melaas, E. K., M. A. Friedl, and Z. Zhu (2013). Detecting interannual variation in deciduous broadleaf forest phenology using Landsat TM/ETM+ data. Remote Sensing of Environment 132:176–185.

Mella-Méndez, I., R. Flores-Peredo, J. D. Amaya-Espinel, B. Bolívar-Cimé, M. C. Mac Swiney G., and A. J. Martínez (2022). Predation of wildlife by domestic cats in a Neotropical city: a multi-factor issue. Biological Invasions. https://doi.org/10.1007/s10530-022-02734-5

Mella-Méndez, I., R. Flores-Peredo, B. Bolívar-Cimé, G. Vázquez-Domínguez, I. Mella-Méndez, R. Flores-Peredo, B. Bolívar-Cimé, and G. Vázquez-Domínguez (2019). Effect of free-ranging dogs and cats on medium-sized wild mammal assemblages in urban protected areas of a Mexican city. Wildlife Research 46:669–678.

Menacho Odio, R. M. (2015). Colisión de aves contra ventanas en Costa Rica: Conociendo el problema a partir de datos de museos, ciencia ciudadana y el aporte de biólogos. Zeledonia 19:10–21.

Metcalfe, N. B., and R. W. Furness (1984). Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. Behavioral Ecology and Sociobiology 15:203–206.

Mikula, P., M. Díaz, T. Albrecht, J. Jokimäki, M.-L. Kaisanlahti-Jokimäki, G. Kroitero, A. P. Møller, P. Tryjanowski, R. Yosef, and M. Hromada (2018). Adjusting risk-taking to the annual cycle of long-distance migratory birds. Scientific Reports 8:13989.

Miller, G., and A. E. Lugo (2009). Guide to the ecological systems of Puerto Rico. U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry IITF-GTR-35.

Miller-Rushing, A. J., T. L. Lloyd-Evans, R. B. Primack, and P. Satzinger (2008). Bird migration times, climate change, and changing population sizes. Global Change Biology 14:1959–1972.

Mirmovitch, V. (1995). Spatial Organisation of Urban Feral Cats (Felis Catus) in Jerusalem. Wildlife Research 22:299.

Mitra, A., C. Chatterjee, and F. Mandal (2018). Synthetic Chemical Pesticides and Their Effects on Birds. Research Journal of Environmental Toxicology 5.

Mohammed, R. S., G. Turner, K. Fowler, M. Pateman, M. A. Nieves-Colón, L. Fanovich, S. B. Cooke, L. M. Dávalos, S. M. Fitzpatrick, C. M. Giovas, M. Stokowski, et al. (2022). Colonial Legacies Influence Biodiversity Lessons: How Past Trade Routes and Power Dynamics Shape Present-Day Scientific Research and Professional Opportunities for Caribbean Scientists. The American Naturalist 200:140–155.

Møller, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. Ecology and Evolution 9:6581–6587.

Moore, F. R. (1994). Resumption of feeding under risk of predation: effect of migratory condition. Animal Behaviour 48:975–977.

Moore, F. R. (2018). Biology of landbird migrants: a stopover perspective. The Wilson Journal of Ornithology 130:1–12.

Moore, F. R., and P. A. Simm (1986). Risk-sensitive foraging by a migratory bird (Dendroica coronata). Experientia 42:1054–1056.

Mora, M. A., D. W. Anderson, and M. E. Mount (1987). Seasonal Variation of Body Condition and Organochlorines in Wild Ducks from California and Mexico. The Journal of Wildlife Management 51:132–141.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, and L. Zhao (2018). Evaluation of sex differences in the stopover behavior and postdeparture movements of wood-warblers. Behavioral Ecology 29:117–127.

Morrissey, C. A., P. Mineau, J. H. Devries, F. Sanchez-Bayo, M. Liess, M. C. Cavallaro, and K. Liber (2015). Neonicotinoid contamination of global surface waters and associated risk to aquatic invertebrates: A review. Environment International 74:291–303.

Mukhin, A., N. Chernetsov, and D. Kishkinev (2008). Acoustic information as a distant cue for habitat recognition by nocturnally migrating passerines during landfall. Behavioral Ecology 19:716–723.

Narango, D. L., D. W. Tallamy, and P. P. Marra (2017). Native plants improve breeding and foraging habitat for an insectivorous bird. Biological Conservation 213:42–50.

Natoli, E. (1985). Spacing pattern in a colony of urban stray cats (Felis catus L.) in the historic centre of Rome. Applied Animal Behaviour Science 14:289–304.

Nebel, S., A. Mills, J. McCracken, and P. Taylor (2010). Declines of Aerial Insectivores in North America Follow a Geographic Gradient. Avian Conservation and Ecology 5.

Nelson, S. B., J. J. Coon, C. J. Duchardt, J. D. Fischer, S. J. Halsey, A. J. Kranz, C. M. Parker, S. C. Schneider, T. M. Swartz, and J. R. Miller (2017). Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. Biological Invasions 19:1547–1563.

Nemes, C. E., S. A. Cabrera-Cruz, M. Anderson, L. W. DeGroote, M. L. Massa, and E. B. Cohen (In Review). More than mortality: Indirect anthropogenic threats to migrating birds. Ornithological Applications.

Németh, Z., and F. R. Moore (2014). Information acquisition during migration: A social perspective. The Auk 131:186–194.

Newsome, T. M., J. A. Dellinger, C. R. Pavey, W. J. Ripple, C. R. Shores, A. J. Wirsing, and C. R. Dickman (2015). The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography 24:1–11.

Newton, I. (2007). Weather-related mass-mortality events in migrants: Weather-related mass-mortality events in migrants. Ibis 149:453–467.

Niedballa, J., R. Sollmann, A. Courtiol, and A. Wilting (2016). camtrapR: an R package for efficient camera trap data management. Methods in Ecology and Evolution 7:1457–1462.

Nilsson, C., R. H. G. Klaassen, and T. Alerstam (2013). Differences in speed and duration of bird migration between spring and autumn. The American Naturalist 181:837–845.

Nilsson, J.-Å., C. Brönmark, L.-A. Hansson, and B. B. Chapman (2014). Individuality in movement: the role of animal personality. In Animal Movement Across Scales (L.-A. Hansson and S. Åkesson, Editors). Oxford University Press, pp. 90–109.

Nimmo, D. G., A. J. R. Carthey, C. J. Jolly, and D. T. Blumstein (2021). Welcome to the Pyrocene: Animal survival in the age of megafire. Global Change Biology 27:5684–5693.

Nogales, M., A. Martin, B. R. Tershy, C. J. Donlan, D. Veitch, N. Puerta, B. Wood, and J. Alonso (2004). A Review of Feral Cat Eradication on Islands. Conservation Biology 18:310–319.

Nogales, M., E. Vidal, F. M. Medina, E. Bonnaud, B. R. Tershy, K. J. Campbell, and E. S. Zavaleta (2013). Feral Cats and Biodiversity Conservation: The Urgent Prioritization of Island Management. BioScience 63:804–810.

Norouzzadeh, M. S., D. Morris, S. Beery, N. Joshi, N. Jojic, and J. Clune (2021). A deep active learning system for species identification and counting in camera trap images. Methods in Ecology and Evolution 12:150–161.

Norris, A. R., L. Frid, C. Debyser, K. L. De Groot, J. Thomas, A. Lee, K. M. Dohms, A. Robinson, W. Easton, K. Martin, and K. L. Cockle (2021). Forecasting the Cumulative Effects of Multiple Stressors on Breeding Habitat for a Steeply Declining Aerial Insectivorous Songbird, the Olive-sided Flycatcher (Contopus cooperi). Frontiers in Ecology and Evolution 9.

Norris, D. R., and C. M. Taylor (2006). Predicting the consequences of carry-over effects for migratory populations. Biology Letters 2:148–151.

Northrup, J. M., J. W. Rivers, Z. Yang, and M. G. Betts (2019). Synergistic effects of climate and land-use change influence broad-scale avian population declines. Global Change Biology 25:1561–1575.

Nytch, C. J., W. C. Hunter, F. Núñez-García, C. Fury, and M. Quiñones (2015). Avian Conservation Planning Priorities for Puerto Rico and the U.S. Virgin Islands (BCR 69).

O'Connell, A. F., J. D. Nichols, and K. U. Karanth (Editors) (2011). Camera Traps in Animal Ecology. Springer Japan, Tokyo.

O'Connell, N. S., L. Dai, Y. Jiang, J. L. Speiser, R. Ward, W. Wei, R. Carroll, and M. Gebregziabher (2017). Methods for Analysis of Pre-Post Data in Clinical Research: A Comparison of Five Common Methods. Journal of biometrics & biostatistics 8:1–8.

Odum, E. P. (1960). Premigratory Hyperphagia in Birds. The American Journal of Clinical Nutrition 8:621–629.

Oguchi, Y., Z. Pohlen, R. J. Smith, and J. C. Owen (2018). Exotic- and native-dominated shrubland habitat use by fall migrating Swainson's Thrushes and Gray Catbirds in Michigan, USA. Condor 120:81–93.

Oguchi, Y., R. J. Smith, and J. C. Owen (2017). Fruits and migrant health: Consequences of stopping over in exotic- vs. native-dominated shrublands on immune and antioxidant status of Swainson's Thrushes and Gray Catbirds. The Condor 119:800–816.

Orduña-Villaseñor, M., D. Valenzuela-Galván, and J. E. Schondube (2023). Tus mejores amigos pueden ser tus peores enemigos: impactos de los gatos y perros domésticos en países megadiversos. Revista Mexicana de Biodiversidad 94:e944850–e944850.

Orłowski, G., and J. Siembieda (2005). Skeletal injuries of Passerines caused by road traffic. Acta Ornithologica 40:15–19.

Ortega, C. P. (2012). Chapter 2: Effects of noise pollution on birds: A brief review of our knowledge. Ornithological Monographs 74:6–22.

Ortega-Álvarez, R., and I. MacGregor-Fors (2009). Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. Landscape and Urban Planning 90:189–195.

Ouyang, J. Q., S. Davies, and D. Dominoni (2018). Hormonally mediated effects of artificial light at night on behavior and fitness: linking endocrine mechanisms with function. Journal of Experimental Biology 221:jeb156893.

Overton, C. T., A. A. Lorenz, E. P. James, R. Ahmadov, J. M. Eadie, F. Mcduie, M. J. Petrie, C. A. Nicolai, M. L. Weaver, D. A. Skalos, S. M. Skalos, et al. (2022). Megafires and thick smoke portend big problems for migratory birds. Ecology 103:e03552.

Owen, J. C., M. C. Garvin, and F. R. Moore (2014). Elevated testosterone advances onset of migratory restlessness in a nearctic-neotropical landbird. Behavioral Ecology and Sociobiology 68:561–569.

Owen, J. C., and F. R. Moore (2006). Seasonal Differences in Immunological Condition of Three Species of Thrushes. The Condor 108:389–398.

Pacheco-Muñoz, R., M. Á. Aguilar-Gómez, and J. E. Schondube (2022a). Overwintering in a megacity: Urban green areas and migratory birds in Mexico City. Urban Forestry & Urban Greening 73:127614.

Pacheco-Muñoz, R., A. Ceja-Madrigal, E. Pérez-Negrón, A. K. Ortiz-Asbun, and J. E. Schondube (2022b). Wintering Town: Individual Quality of Migratory Warblers Using Green Urban Areas in a Neotropical City. Frontiers in Ecology and Evolution 9.

Pain, D. J., R. Mateo, and R. E. Green (2019). Effects of lead from ammunition on birds and other wildlife: A review and update. Ambio 48:935–953.

Palmer, M. S., K. M. Gaynor, J. A. Becker, J. O. Abraham, M. A. Mumma, and R. M. Pringle (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. Trends in Ecology & Evolution 37:911–925.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Parmesan, C., and G. Yohe (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Parrish, J. D. (2000). Behavioral, energetic, and conservation implications of foraging plasticity during migration. Studies in Avian Biology 20:53–70.

Patricelli, G. L., and J. L. Blickley (2006). Avian Communication in Urban Noise: Causes and Consequences of Vocal Adjustment. The Auk 123:639–649.

Pattee, O. H., and D. J. Pain (2002). Lead in the Environment. In Handbook of Ecotoxicology. CRC Press.

Paxton, E. H., S. L. Durst, M. K. Sogge, T. J. Koronkiewicz, and K. L. Paxton (2017). Survivorship across the annual cycle of a migratory passerine, the willow flycatcher. Journal of Avian Biology 48:1126–1131.

Paxton, K. L., E. B. Cohen, E. H. Paxton, Z. Németh, and F. R. Moore (2014). El Niño-Southern Oscillation Is Linked to Decreased Energetic Condition in Long-Distance Migrants. PLoS ONE 9:e95383.

Paxton, K. L., and F. R. Moore (2017). Connecting the dots: Stopover strategies of an intercontinental migratory songbird in the context of the annual cycle. Ecology and Evolution 7:6716–6728.

Pearce-Higgins, J. W., D. J. Brown, D. J. T. Douglas, J. A. Alves, M. Bellio, P. Bocher, G. M. Buchanan, R. P. Clay, J. Conklin, N. Crockford, P. Dann, et al. (2017). A global threats overview for Numeniini populations: synthesising expert knowledge for a group of declining migratory birds. Bird Conservation International 27:6–34.

Pearce-Higgins, J. W., and R. E. Green (2014). Birds and Climate Change: Impacts and Conservation Responses. Cambridge University Press.

Pechony, O., and D. T. Shindell (2010). Driving forces of global wildfires over the past millennium and the forthcoming century. Proceedings of the National Academy of Sciences 107:19167–19170.

Perold, V., S. Ralston-Paton, and P. Ryan (2020). On a collision course? The large diversity of birds killed by wind turbines in South Africa. Ostrich 91:228–239.

Pettinga, D., J. Kennedy, and D. Proppe (2015). Common urban birds continue to perceive predator calls that are overlapped by road noise. Urban Ecosystems 19.

Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. Chr. Stenseth (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Pimentel, D. (2005). 'Environmental and Economic Costs of the Application of Pesticides Primarily in the United States.' Environment, Development and Sustainability 7:229–252.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team (2020). nlme: Linear and nonlinear mixed effects models. [Online.] Available at https://CRAN.R-project.org/package=nlme.

Pinto, F. A. S., A. P. Clevenger, and C. Grilo (2020). Effects of roads on terrestrial vertebrate species in Latin America. Environmental Impact Assessment Review 81:106337.

Polgar, C. A., and R. B. Primack (2011). Leaf-out phenology of temperate woody plants: from trees to ecosystems. New Phytologist 191:926–941.

Pomeroy, A. C., D. A. Acevedo Seaman, R. W. Butler, R. W. Elner, T. D. Williams, and R. C. Ydenberg (2008). Feeding-Danger Trade-Offs Underlie Stopover Site Selection by Migrants. Avian Conservation and Ecology 3:art7.

Pomeroy, A. C., R. W. Butler, and R. C. Ydenberg (2006). Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. Behavioral Ecology 17:1041–1045.

Poot, H., B. J. Ens, H. de Vries, M. A. H. Donners, M. R. Wernand, and J. M. Marquenie (2008). Green light for nocturnally migrating birds. Ecology And Society 13:47–47.

Porneluzi, P., M. A. Van Horn, and T. M. Donovan (2020). Ovenbird (Seiurus aurocapilla), version 1.0. Birds of the World. https://doi.org/10.2173/bow.ovenbi1.01

Powell, L. L., A. Metallo, C. Jarrett, N. W. Cooper, P. P. Marra, S. R. McWilliams, U. Bauchinger, and B. C. Dossman (2021). An inexpensive, 3D-printable breast muscle meter for field ornithologists. Journal of Field Ornithology 92:67–76.

Preisser, E. L., D. I. Bolnick, and M. F. Benard (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501–509.

Puga-Caballero, A., I. MacGregor-Fors, and R. Ortega-Álvarez (2014). Birds at the urban fringe: avian community shifts in different peri-urban ecotones of a megacity. Ecological Research 29:619–628.

R Core Team (2020). R: A language and environment for statistical computing. [Online.] Available at https://www.R-project.org/.

Raim, A. (1978). A Radio Transmitter Attachment for Small Passerine Birds. Bird-Banding 49:326–332.

Raja, N. B. (2022). Colonialism shaped today's biodiversity. Nature Ecology & Evolution 6:1597–1598.

Ramirez Jr., P., K. Dickerson, J. Lindstrom, C. U. Meteyer, and S. Darrah (2015). Lapland longspur mortality at an oil well drilling rig site, Laramie County, Wyoming. Wildlife Society Bulletin 39:165–168.

Ramos-González, O. M. (2014). The green areas of San Juan, Puerto Rico. Ecology and Society 19:art21.

Rappole, J. H., and A. R. Tipton (1991). New Harness Design for Attachment of Radio Transmitters to Small Passerines. Journal of Field Ornithology 62:335–337.

Ratikainen, I. I., J. A. Gill, T. G. Gunnarsson, W. J. Sutherland, and H. Kokko (2007). When density dependence is not instantaneous: theoretical developments and management implications. Ecology Letters 0:071104194519001-???

Rebke, M., V. Dierschke, C. N. Weiner, R. Aumüller, K. Hill, and R. Hill (2019). Attraction of nocturnally migrating birds to artificial light: The influence of colour, intensity and blinking mode under different cloud cover conditions. Biological Conservation 233:220–227.

Rebolo-Ifrán, N., L. Zamora-Nasca, and S. A. Lambertucci (2021). Cat and dog predation on birds: The importance of indirect predation after bird-window collisions. Perspectives in Ecology and Conservation 19:293–299.

Redmond, L. J., C. Eroh, J. I. Haq, and D. Varra (2020). The effect of offspring value on variation of nest defense intensity in gray catbirds (Dumetella carolinensis). Behavioral Ecology and Sociobiology 74:30.

Reece, R. L., and P. Handson (1982). Observations on the accidental poisoning of birds by organophosphate insecticides and other toxic substances. The Veterinary record 111:453–455.

Rich, C., and T. Longcore (2006). Ecological consequences of artificial night lighting. Island Press, Washington, D. C.

Richard, F.-J., I. Southern, M. Gigauri, G. Bellini, O. Rojas, and A. Runde (2021). Warning on nine pollutants and their effects on avian communities. Global Ecology and Conservation 32:e01898.

Rimmer, C. C., K. P. McFarland, D. C. Evers, E. K. Miller, Y. Aubry, D. Busby, and R. J. Taylor (2005). Mercury Concentrations in Bicknell?s Thrush and Other Insectivorous Passerines in Montane Forests of Northeastern North America. Ecotoxicology 14:223–240.

van Riper, C., S. L. Puckett, and A. J. Darrah (2018). Influences of the invasive tamarisk leaf beetle (Diorhabda carinulata) on avian diets along the Dolores River in Southwestern Colorado USA. Biological Invasions 20:3145–3159.

Robart, A. R., M. M. K. McGuire, and H. E. Watts (2018). Increasing photoperiod stimulates the initiation of spring migratory behaviour and physiology in a facultative migrant, the pine siskin. Royal Society Open Science 5:180876.

Robbins, C. S. (1981). Effect of time of day on bird activity. Studies in Avian Biology 6:275–286.

Robinson, R., H. Crick, J. Learmonth, I. Maclean, C. Thomas, F. Bairlein, M. Forchhammer, C. Francis, J. Gill, B. Godley, J. Harwood, et al. (2009). Travelling through a warming world: climate change and migratory species. Endangered Species Research 7:87–99.

Rockwell, S. M., J. M. Wunderle, T. S. Sillett, C. I. Bocetti, D. N. Ewert, D. Currie, J. D. White, and P. P. Marra (2017a). Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. Oecologia 183:715–726.

Rockwell, S. M., J. M. Wunderle, T. S. Sillett, C. I. Bocetti, D. N. Ewert, D. Currie, J. D. White, and P. P. Marra (2017b). Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. Oecologia 183:715–726.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack (2011). Anthropogenic resource subsidies decouple predator–prey relationships. Ecological Applications 21:936–943.

Rodríguez-Durán, A. (1996). Foraging Ecology of the Puerto Rican Boa (Epicrates inornatus): Bat Predation, Carrion Feeding, and Piracy. Journal of Herpetology 30:533–536.

Rodríguez-Durán, A., J. Pérez, M. A. Montalbán, and J. M. Sandoval (2010). Predation by Free-Roaming Cats on an Insular Population of Bats. Acta Chiropterologica 12:359–362.

Rodriguez-Sanchez, F. (2022). rSDM: Species distribution and niche modelling in R. https://github.com/Pakillo/rSDM.

Rogers, S. E., B. W. Cornaby, C. W. Rodman, P. R. Sticksel, and D. A. Tolle (1977). Environmental studies related to the operation of wind energy conversion systems. Final report. Battelle Columbus Labs., OH (USA).

Romano, A., L. Z. Garamszegi, D. Rubolini, and R. Ambrosini (2022). Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: A global meta-analysis. Ecological Monographs n/a:e1552.

Ronconi, R. A., K. A. Allard, and P. D. Taylor (2015). Bird interactions with offshore oil and gas platforms: Review of impacts and monitoring techniques. Journal of Environmental Management 147:34–45.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra (2019). Decline of the North American avifauna. Science 366:120–124.

Rosenzweig, C., D. Karoly, M. Vicarelli, P. Neofotis, Q. Wu, G. Casassa, A. Menzel, T. L. Root, N. Estrella, B. Seguin, P. Tryjanowski, et al. (2008). Attributing physical and biological impacts to anthropogenic climate change. Nature 453:353–357.

Roux, K. E., and P. P. Marra (2007). The Presence and Impact of Environmental Lead in Passerine Birds Along an Urban to Rural Land Use Gradient. Archives of Environmental Contamination and Toxicology 53:261–268.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner (2013). Spatial Capture-Recapture. Academic Press.

Ruegg, K. C., E. C. Anderson, K. L. Paxton, V. Apkenas, S. Lao, R. B. Siegel, D. F. DeSante, F. Moore, and T. B. Smith (2014). Mapping migration in a songbird using high-resolution genetic markers. Molecular Ecology 23:5726–5739.

Ruegg, K. C., R. J. Hijmans, and C. Moritz (2006). Climate change and the origin of migratory pathways in the Swainson's thrush, Catharus ustulatus. Journal of Biogeography 33:1172–1182.

Ruelas Inzunza, E., K. L. Cockle, M. G. Núñez Montellano, C. S. Fontana, C. Cuatianquiz Lima, M. A. Echeverry-Galvis, R. A. Fernández-Gómez, F. A. Montaño-Centellas, E. Bonaccorso, S. A. Lambertucci, C. Cornelius, et al. (2023). How to include and recognize the work of ornithologists based in the Neotropics: Fourteen actions for Ornithological Applications, Ornithology, and other global-scope journals. Ornithological Applications:duac047.

Runge, C. A., E. Gallo-Cajiao, M. J. Carey, S. T. Garnett, R. A. Fuller, and P. C. McCormack (2017). Coordinating Domestic Legislation and International Agreements to Conserve Migratory Species: A Case Study from Australia. Conservation Letters 10:765–772.

Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis, and R. A. Fuller (2014). Conserving mobile species. Frontiers in Ecology and the Environment 12:395–402.

Runge, C. A., A. I. T. Tulloch, H. P. Possingham, V. J. D. Tulloch, and R. A. Fuller (2016). Incorporating dynamic distributions into spatial prioritization. Diversity and Distributions 22:332–343.

Runge, C. A., J. E. M. Watson, S. H. M. Butchart, J. O. Hanson, H. P. Possingham, and R. A. Fuller (2015). Protected areas and global conservation of migratory birds. Science 350:1255–1258.

Rushing, C. S., J. A. Hostetler, T. S. Sillett, P. P. Marra, J. A. Rotenberg, and T. B. Ryder (2017). Spatial and temporal drivers of avian population dynamics across the annual cycle. Ecology 98:2837–2850.

Ryder, T. B., J. W. Fox, and P. P. Marra (2011). Estimating Migratory Connectivity of Gray Catbirds ( *Dumetella carolinensis* ) using Geolocator and Mark–recapture Data. The Auk 128:448–453.

Saino, N., R. Ambrosini, D. Rubolini, J. von Hardenberg, A. Provenzale, K. Hüppop, O. Hüppop, A. Lehikoinen, E. Lehikoinen, K. Rainio, M. Romano, and L. Sokolov (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society B: Biological Sciences 278:835–842.

Samraoui, B., Y. Kayser, L. Touati, F. Samraoui, A. Boucheker, H. A. El-Serehy, and K. R. Samraoui (2022). Diet of breeding Eleonora's falcon Falco eleonorae in Algeria: Insights for the autumn trans-Mediterranean avian migration. Ecology and Evolution 12:e9065.

Samuels, B., B. Fenton, E. Fernández-Juricic, and S. A. MacDougall-Shackleton (2022). Opening the black box of bird-window collisions: passive video recordings in a residential backyard. PeerJ 10:e14604.

Sánchez-Bayo, F., and K. A. G. Wyckhuys (2019). Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232:8–27.

Sandberg, R., and F. R. Moore (1996). Fat Stores and Arrival on the Breeding Grounds: Reproductive Consequences for Passerine Migrants. Oikos 77:577–581.

Sanderfoot, O. V., S. B. Bassing, J. L. Brusa, R. L. Emmet, S. J. Gillman, K. Swift, and B. Gardner (2021). A review of the effects of wildfire smoke on the health and behavior of wildlife. Environmental Research Letters 16:123003.

Sanderfoot, O. V., and T. Holloway (2017). Air pollution impacts on avian species via inhalation exposure and associated outcomes. Environmental Research Letters 12:083002.

Sandifer, P. A., A. E. Sutton-Grier, and B. P. Ward (2015). Exploring connections among nature, biodiversity, ecosystem services, and human health and well-being: Opportunities to enhance health and biodiversity conservation. Ecosystem Services 12:1–15.

Santiago-Alarcon, D., and C. A. Delgado-V (2017). Warning! Urban Threats for Birds in Latin America. In Avian Ecology in Latin American Cityscapes (I. MacGregor-Fors and J. F. Escobar-Ibáñez, Editors). Springer International Publishing, Cham, pp. 125–142.

Santos, L. P. S., V. F. de Abreu, and M. F. de Vasconcelos (2017). Bird mortality due to collisions in glass panes on an Important Bird Area of southeastern Brazil. Revista Brasileira de Ornitologia - Brazilian Journal of Ornithology 25:90–101.

Saunders, S. P., J. X. Wu, E. A. Gow, E. Adams, B. L. Bateman, T. Bayard, S. Beilke, A. A. Dayer, A. M. V. Fournier, K. Fox, P. Heglund, et al. (2021). Bridging the research-implementation gap in avian conservation with translational ecology. Ornithological Applications 123:duab018.

Schaub, M., and L. Jenni (2000). Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

Schmaljohann, H., and C. Both (2017). The limits of modifying migration speed to adjust to climate change. Nature Climate Change 7:573–576.

Schmaljohann, H., and V. Dierschke (2005). Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*: *Optimal bird migration and predation risk*. Journal of Animal Ecology 74:131–138.

Schmaljohann, H., C. Eikenaar, and N. Sapir (2022). Understanding the ecological and evolutionary function of stopover in migrating birds. Biological Reviews n/a.

Schmaljohann, H., S. Lisovski, and F. Bairlein (2017). Flexible reaction norms to environmental variables along the migration route and the significance of stopover duration for total speed of migration in a songbird migrant. Frontiers in Zoology 14:17.

Schwartz, M. D., T. R. Ault, and J. L. Betancourt (2013). Spring onset variations and trends in the continental United States: past and regional assessment using temperature-based indices. International Journal of Climatology 33:2917–2922.

Seabloom, R. W., G. L. Pearson, L. W. Oring, and J. R. Reilly (1973). AN INCIDENT OF FENTHION MOSQUITO CONTROL AND SUBSEQUENT AVIAN MORTALITY. Journal of Wildlife Diseases 9:18–20.

Sedano-Cruz, R. (2022). Estimated number of birds killed by domestic cats in Colombia. Avian Conservation and Ecology 17.

Seewagen, C. L. (2020). The threat of global mercury pollution to bird migration: potential mechanisms and current evidence. Ecotoxicology 29:1254–1267.

Seewagen, C. L., D. A. Cristol, and A. R. Gerson (2016). Mobilization of mercury from lean tissues during simulated migratory fasting in a model songbird. Scientific Reports 6:25762.

Seewagen, C. L., C. R. Elowe, A. R. Gerson, D. J. E. Groom, Y. Ma, M. Yildirim, and C. G. Guglielmo (2022). Short-term mercury exposure disrupts muscular and hepatic lipid metabolism in a migrant songbird. Scientific Reports 12:11470.

Seewagen, C. L., and C. G. Guglielmo (2010). Effects of Fat and Lean Body Mass on Migratory Landbird Stopover Duration. The Wilson Journal of Ornithology 122:82–87.

Seewagen, C. L., and C. G. Guglielmo (2011). Quantitative magnetic resonance analysis and a morphometric predictive model reveal lean body mass changes in migrating Nearctic–Neotropical passerines. Journal of Comparative Physiology B 181:413–421.

Seewagen, C. L., C. G. Guglielmo, and Y. E. Morbey (2013). Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. Behavioral Ecology 24:634–642.

Seewagen, C. L., and E. J. Slayton (2008). Mass Changes Of Migratory Landbirds During Stopovers In A New York City Park. The Wilson Journal of Ornithology 120:296–303.

Seewagen, C. L., E. J. Slayton, and C. G. Guglielmo (2010). Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecologica 36:484–492.

Şekercioğlu, Ç. H., D. G. Wenny, C. J. Whelan, and C. Floyd (2016). Why birds matter: Bird ecosystem services promote biodiversity and human well-being. In Why Birds Matter: Avian Ecological Functions and Ecosystem Services. University of Chicago Press.

Senner, N. R., J. R. Conklin, and T. Piersma (2015). An ontogenetic perspective on individual differences. Proceedings of the Royal Society B: Biological Sciences 282:20151050.

Seto, K. C., M. Fragkias, B. Güneralp, and M. K. Reilly (2011). A Meta-Analysis of Global Urban Land Expansion. PLOS ONE 6:e23777.

Seymour, C. L., R. E. Simmons, F. Morling, S. T. George, K. Peters, and M. J. O'Riain (2020). Caught on camera: The impacts of urban domestic cats on wild prey in an African city and neighbouring protected areas. Global Ecology and Conservation 23:e01198.

Shannon, G., M. F. McKenna, L. M. Angeloni, K. R. Crooks, K. M. Fristrup, E. Brown, K. A. Warner, M. D. Nelson, C. White, J. Briggs, S. McFarland, and G. Wittemyer (2016). A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91:982–1005.

Shariatinajafabadi, M., T. Wang, A. K. Skidmore, A. G. Toxopeus, A. Kölzsch, B. A. Nolet, K.-M. Exo, L. Griffin, J. Stahl, and D. Cabot (2014). Migratory Herbivorous Waterfowl Track Satellite-Derived Green Wave Index. PLoS ONE 9:e108331.

Sheehy, J., C. M. Taylor, and D. R. Norris (2011). The importance of stopover habitat for developing effective conservation strategies for migratory animals. Journal of Ornithology 152:161–168.

Sillett, T. S., and R. T. Holmes (2002a). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Sillett, T. S., and R. T. Holmes (2002b). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Sims, V., K. L. Evans, S. E. Newson, J. A. Tratalos, and K. J. Gaston (2008). Avian assemblage structure and domestic cat densities in urban environments. Diversity and Distributions 14:387–399.

Slabbekoorn, H., R. J. Dooling, A. N. Popper, and R. R. Fay (2018). Effects of Anthropogenic Noise on Animals. Springer.

van der Sluijs, J. P. (2020). Insect decline, an emerging global environmental risk. Current Opinion in Environmental Sustainability 46:39–42.

Smith, R. A., M. Gagné, and K. C. Fraser (2021). Pre-migration artificial light at night advances the spring migration timing of a trans-hemispheric migratory songbird. Environmental Pollution 269:116136.

Smith, R. J., M. I. Hatch, and D. A. Cimprich (2020). Gray Catbird (Dumetella carolinensis). *Birds of the World*. [Online.] Available at https://doi.org/10.2173/bow.grycat.01.

Smith, R. J., and F. R. Moore (2005a). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Smith, R. J., and F. R. Moore (2005b). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Smith, S. B., S. A. DeSando, and T. Pagano (2013). The Value of Native and Invasive Fruit-Bearing Shrubs for Migrating Songbirds. Northeastern Naturalist 20:171–184.

Smith, S. B., and S. R. McWilliams (2010). Patterns of Fuel Use and Storage in Migrating Passerines in Relation to Fruit Resources at Autumn Stopover Sites. The Auk 127:108–118.

Smith, S. B., A. C. Miller, C. R. Merchant, and A. F. Sankoh (2015). Local site variation in stopover physiology of migrating songbirds near the south shore of Lake Ontario is linked to fruit availability and quality. Conservation Physiology 3:cov036.

Smolinsky, J. A., R. H. Diehl, T. A. Radzio, D. K. Delaney, and F. R. Moore (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behavioral Ecology and Sociobiology 67:2041–2051.

Soares, L., K. Cockle, E. Ruelas Inzunza, J. Ibarra, C. Miño, S. Zuluaga, E. Bonaccorso, J. Ríos-Orjuela, F. Montano-Centellas, and J. Freile (2023). Neotropical Ornithology: Reckoning with historical assumptions, removing systemic barriers, and reimagining the future. https://doi.org/10.32942/OSF.IO/YU2FX

Sodhi, N. S. (2002). Competition in the Air: Birds Versus Aircraft. The Auk 119:587–595.

Somveille, M., A. Manica, S. H. M. Butchart, and A. S. L. Rodrigues (2013). Mapping global diversity patterns for migratory birds. PloS one 8:e70907–e70907.

Spear, D., L. C. Foxcroft, H. Bezuidenhout, and M. A. McGeoch (2013). Human population density explains alien species richness in protected areas. Biological Conservation 159:137–147.

Spiker, C. J. (1927). Feathered Victims of the Automobile. Wilson Bulletin 39:11–12.

Spiller, K. J., and R. Dettmers (2019). Evidence for multiple drivers of aerial insectivore declines in North America. The Condor 121:duz010.

Stanton, R. L., C. A. Morrissey, and R. G. Clark (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agriculture, Ecosystems & Environment 254:244–254.

Stehle, S., S. Bub, and R. Schulz (2018). Compilation and analysis of global surface water concentrations for individual insecticide compounds. Science of The Total Environment 639:516–525.

Stobo-Wilson, A. M., B. P. Murphy, S. M. Legge, H. Caceres-Escobar, D. G. Chapple, H. M. Crawford, S. J. Dawson, C. R. Dickman, T. S. Doherty, P. A. Fleming, S. T. Garnett, et al. (2022). Counting the bodies: Estimating the numbers and spatial variation of Australian reptiles, birds and mammals killed by two invasive mesopredators. Diversity and Distributions 28:976–991.

Stone, W. (1906). Some light on night migration. Auk 23:249–252.

Stoner, D. (1936). Wildlife Casualties on the Highways. Wilson Bulletin 48:276–283.

Streby, H. M., T. L. McAllister, S. M. Peterson, G. R. Kramer, J. A. Lehman, and D. E. Andersen (2015). Minimizing marker mass and handling time when attaching radio-transmitters and geolocators to small songbirds. The Condor 117:249–255.

Studds, C. E., and P. P. Marra (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society B: Biological Sciences 278:3437–3443.

Studds, C., and P. Marra (2007). Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, Setophaga ruticilla. Climate Research 35:115–122.

Sutherland, C., J. A. Royle, and D. W. Linden (2019). oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. Ecography 42:1459–1469.

Swanson, A., M. Kosmala, C. Lintott, R. Simpson, A. Smith, and C. Packer (2015). Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. Scientific Data 2:150026.

Szabo, J. K., C.-Y. Choi, R. S. Clemens, B. Hansen, J. K. Szabo, C.-Y. Choi, R. S. Clemens, and B. Hansen (2016). Conservation without borders – solutions to declines of migratory shorebirds in the East Asian–Australasian Flyway. Emu 116:215–221.

Tanabe, S., K. Senthilkumar, K. Kannan, and A. N. Subramanian (1998). Accumulation Features of Polychlorinated Biphenyls and Organochlorine Pesticides in Resident and Migratory Birds from South India. Archives of Environmental Contamination and Toxicology 34:387–397.

Tanaka, H., H. Ogi, S. Tanabe, R. Tatsukawa, and N. Oka (1986). Bioaccumulation and metabolism of PCBs and DDE in Short-tailed Shearwater Puffinus tenuirostris during its transequatorial migration and in the wintering and breeding grounds. Memoirs of National Institute of Polar Research.

Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, et al. (2017). The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:art8.

Thorup, K., A. P. Tøttrup, M. Willemoes, R. H. G. Klaassen, R. Strandberg, M. L. Vega, H. P. Dasari, M. B. Araújo, M. Wikelski, and C. Rahbek (2017). Resource tracking within and across continents in long-distance bird migrants. Science Advances 3:e1601360.

Tomas, W. M., C. N. Berlinck, R. M. Chiaravalloti, G. P. Faggioni, C. Strüssmann, R. Libonati, C. R. Abrahão, G. do Valle Alvarenga, A. E. de Faria Bacellar, F. R. de Queiroz Batista, T. S. Bornato, et al. (2021). Distance sampling surveys reveal 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal, Brazil. Scientific Reports 11:23547.

Tonra, C. M., P. P. Marra, and R. L. Holberton (2011). Early elevation of testosterone advances migratory preparation in a songbird. Journal of Experimental Biology 214:2761–2767.

Tøttrup, A. P., R. H. G. Klaassen, M. W. Kristensen, R. Strandberg, Y. Vardanis, Å. Lindström, C. Rahbek, T. Alerstam, and K. Thorup (2012). Drought in Africa caused delayed arrival of European songbirds. Science 338:1307–1307.

Tøttrup, A. P., K. Rainio, T. Coppack, E. Lehikoinen, C. Rahbek, and K. Thorup (2010). Local Temperature Fine-Tunes the Timing of Spring Migration in Birds. Integrative and Comparative Biology 50:293–304.

Townsend, A. K., A. B. Clark, and K. J. McGowan (2011). Injury and paternity loss in cooperatively breeding American Crows. Journal of Field Ornithology 82:415–421.

Travers, M., S. Driskill, A. Stemen, T. Geelhoed, D. Golden, S. Koike, A. Shipley, H. Moon, T. Anderson, M. Bache, and A. Raine (2021). Post-collision impacts, crippling bias, and environmental bias in a study of Newell's Shearwater and Hawaiian Petrel powerline collisions. Avian Conservation and Ecology 16.

Tryjanowski, P., F. Morelli, P. Skórka, A. Goławski, P. Indykiewicz, A. Pape Møller, C. Mitrus, D. Wysocki, and P. Zduniak (2015). Who started first? Bird species visiting novel birdfeeders. Scientific Reports 5:11858.

Tuia, D., B. Kellenberger, S. Beery, B. R. Costelloe, S. Zuffi, B. Risse, A. Mathis, M. W. Mathis, F. van Langevelde, T. Burghardt, R. Kays, et al. (2022). Perspectives in machine learning for wildlife conservation. Nature Communications 13:792.

Tulloch, V. J., A. I. Tulloch, P. Visconti, B. S. Halpern, J. E. Watson, M. C. Evans, N. A. Auerbach, M. Barnes, M. Beger, I. Chadès, S. Giakoumi, et al. (2015). Why do we map threats? Linking threat mapping with actions to make better conservation decisions. Frontiers in Ecology and the Environment 13:91–99.

Tyler, R. K., K. M. Winchell, and L. J. Revell (2016). Tails of the City: Caudal Autotomy in the Tropical Lizard, Anolis cristatellus, in Urban and Natural Areas of Puerto Rico. Journal of Herpetology 50:435–441.

Uddin, M., S. Dutta, V. Kolipakam, H. Sharma, F. Usmani, and Y. Jhala (2021). High bird mortality due to power lines invokes urgent environmental mitigation in a tropical desert. Biological Conservation 261:109262.

Underwood, T. J., and R. M. Underwood (2013). Bird behaviour on and entanglement in invasive burdock (Arctium spp.) plants in Winnipeg, Manitoba. The Canadian Field-Naturalist 127:164–174.

Usui, T., S. H. M. Butchart, and A. B. Phillimore (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. Journal of Animal Ecology 86:250–261.

Vallverdú-Coll, N., M. E. Ortiz-Santaliestra, F. Mougeot, D. Vidal, and R. Mateo (2015). Sublethal Pb Exposure Produces Season-Dependent Effects on Immune Response, Oxidative Balance and Investment in Carotenoid-based Coloration in Red-Legged Partridges. Environmental Science & Technology 49:3839–3850.

Van Doren, B. M., K. G. Horton, A. M. Dokter, H. Klinck, S. B. Elbin, and A. Farnsworth (2017). High-intensity urban light installation dramatically alters nocturnal bird migration. Proceedings of the National Academy of Sciences 114:11175–11180.

Van Doren, B. M., D. E. Willard, M. Hennen, K. G. Horton, E. F. Stuber, D. Sheldon, A. H. Sivakumar, J. Wang, A. Farnsworth, and B. M. Winger (2021). Drivers of fatal bird collisions in an urban center. Proceedings of the National Academy of Sciences 118:e2101666118.

Vázquez-Plass, E. O., and J. M. Wunderle, Jr. (2013). Avian distribution along a gradient of urbanization in northeastern Puerto Rico. ECOLOGICAL BULLETINS:16.

Venables, W. N., and B. D. Ripley (2002). Modern Applied Statistics with S. Fourth. Springer, New York, NY.

Vickery, J. A., S. R. Ewing, K. W. Smith, D. J. Pain, F. Bairlein, J. Škorpilová, and R. D. Gregory (2014). The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156:1–22.

Villanueva, C., G. Prado, W. Gould, C. García-Quijano, and J. Kolbe (2022). Interviews with farmers suggest negative direct and indirect effects of the invasive green iguana (Iguana iguana) on agriculture in Puerto Rico. Management of Biological Invasions 13:781–797.

Visser, M. E., A. C. Perdeck, J. H. Van BALEN, and C. Both (2009). Climate change leads to decreasing bird migration distances. Global Change Biology 15:1859–1865.

Voelkl, B., J. A. Firth, and B. C. Sheldon (2016). Nonlethal predator effects on the turn-over of wild bird flocks. Scientific Reports 6:33476.

de Vos, A., and M. W. Schwartz (2022). Confronting parachute science in conservation. Conservation Science and Practice 4:e12681.

Vyas, N. B., E. F. Hill, J. R. Sauer, and W. J. Kuenzel (1995). Acephate affects migratory orientation of the white-throated sparrow (Zonotrichia albicollis). Environmental Toxicology and Chemistry 14:1961–1965.

Wald, D. M., S. K. Jacobson, and J. K. Levy (2013). Outdoor cats: Identifying differences between stakeholder beliefs, perceived impacts, risk and management. Biological Conservation 167:414–424.

Walker, H. A. (2008). Floristics and physiognomy determine migrant landbird response to Tamarisk (Tamarix ramosissima) invasion in riparian areas. Auk 125:520–531.

Ware, H. E., C. J. W. McClure, J. D. Carlisle, and J. R. Barber (2015). A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. PNAS 112:12105–12109.

Weber, T. P., A. I. Houston, and B. J. Ens (1999). Consequences of Habitat Loss at Migratory Stopover Sites: A Theoretical Investigation. Journal of Avian Biology 30:416–426.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

Westerling, A. L. (2016). Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150178.

Westerling, A. L., A. Gershunov, T. J. Brown, D. R. Cayan, and M. D. Dettinger (2003). Climate and Wildfire in the Western United States. Bulletin of the American Meteorological Society 84:595–604.

Whelan, R., L. Rodgerson, and C. R. Dickman (2002). Developing a process-based understanding of population changes in fire-prone landscapes. In Flammable Australia: The fire regimes and biodiversity of a continent.

Whitaker, D. M., and S. W. Eaton (2020). Northern Waterthrush (Parkesia noveboracensis), version 1.0. Birds of the World. https://doi.org/10.2173/bow.norwat.01

Whitaker, D. M., I. G. Warkentin, J. P. B. McDermott, P. E. Lowther, C. C. Rimmer, B. Kessel, S. L. Johnson, and W. G. Ellison (2020). Gray-cheeked Thrush (Catharus minimus), version 1.0. Birds of the World. https://doi.org/10.2173/bow.gycthr.01

White, F. B. (1927). Birds and Motor Cars. The Auk 44:265–266.

White, K., J. Pontius, and P. Schaberg (2014). Remote sensing of spring phenology in northeastern forests: A comparison of methods, field metrics and sources of uncertainty. Remote Sensing of Environment 148:97–107.

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wilcove, D. S., and M. Wikelski (2008). Going, Going, Gone: Is Animal Migration Disappearing. PLoS Biology 6:e188.

Williams, R. J., S. D. Holladay, S. M. Williams, and R. M. Gogal (2018). Environmental Lead and Wild Birds: A Review. In Reviews of Environmental Contamination and Toxicology Volume 245 (P. de Voogt, Editor). Springer International Publishing, Cham, pp. 157–180.

Wilson, A. A., M. A. Ditmer, J. R. Barber, N. H. Carter, E. T. Miller, L. P. Tyrrell, and C. D. Francis (2021). Artificial night light and anthropogenic noise interact to influence bird abundance over a continental scale. Global Change Biology 27:3987–4004.

Wilson, K. A., N. A. Auerbach, K. Sam, A. G. Magini, A. S. L. Moss, S. D. Langhans, S. Budiharta, D. Terzano, and E. Meijaard (2016). Conservation Research Is Not Happening Where It Is Most Needed. PLOS Biology 14:e1002413.

Wilson, M. W., A. D. Ridlon, K. M. Gaynor, S. D. Gaines, A. C. Stier, and B. S. Halpern (2020). Ecological impacts of human-induced animal behaviour change. Ecology Letters 23:1522–1536.

Winger, B. M., G. G. Auteri, T. M. Pegan, and B. C. Weeks (2019a). A long winter for the Red Queen: rethinking the evolution of seasonal migration. Biological Reviews 94:737–752.

Winger, B. M., B. C. Weeks, A. Farnsworth, A. W. Jones, M. Hennen, and D. E. Willard (2019b). Nocturnal flight-calling behaviour predicts vulnerability to artificial light in migratory birds. Proceedings of the Royal Society B: Biological Sciences 286:20190364.

With, K. A. (2002). The Landscape Ecology of Invasive Spread. Conservation Biology 16:1192–1203.

Woinarski, J. C. Z., B. P. Murphy, S. M. Legge, S. T. Garnett, M. J. Lawes, S. Comer, C. R. Dickman, T. S. Doherty, G. Edwards, A. Nankivell, D. Paton, et al. (2017). How many birds are killed by cats in Australia? Biological Conservation 214:76–87.

Wood, E. M., and A. M. Pidgeon (2015). Climatic Extremes Influence Spring Tree Phenology and Migratory Songbird Foraging Behavior. In Phenological Synchrony and Bird Migration (E. M. Wood and J. L. Kellermann, Editors). 0 edition. CRC Press, pp. 132–147.

Wunderle, J. M., and R. B. Waide (1994). Future prospects for Nearctic migrants wintering in Caribbean forests. Bird Conservation International 4:191–207.

Wunderle, Jr., J. M. (2008). From the past to the globalized future for Caribbean birds. Journal of Caribbean Ornithology 21:69–79.

Xu, Y., M. Kieboom, R. van lammeren, Y. Si, and W. Boer (2020). Indicators of site loss from a migration network: Anthropogenic factors influence waterfowl movement patterns at stopover sites. Global Ecology and Conservation 25:e01435.

Yamaura, Y., H. Schmaljohann, S. Lisovski, M. Senzaki, K. Kawamura, Y. Fujimaki, and F. Nakamura (2017). Tracking the Stejneger's stonechat Saxicola stejnegeri along the East Asian–Australian Flyway from Japan via China to southeast Asia. Journal of Avian Biology 48:197–202.

Yang, D., A. Yang, J. Yang, R. Xu, and H. Qiu (2021). Unprecedented Migratory Bird Die-Off: A Citizen-Based Analysis on the Spatiotemporal Patterns of Mass Mortality Events in the Western United States. GeoHealth 5:e2021GH000395.

Ydenberg, R. C. (2022). Seasonal and inter-annual variation in exposure to peregrines (Falco peregrinus) for southbound western sandpipers (Calidris mauri). Movement Ecology 10:1–7.

Ydenberg, R. C., R. W. Butler, and D. B. Lank (2007). Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. Journal of Avian Biology 38:523–529.

Ydenberg, R. C., and L. M. Dill (1986). The economics of fleeing from predators. Advances in the Study of Behavior 16.

Yong, D. L., W. Heim, S. U. Chowdhury, C.-Y. Choi, P. Ktitorov, O. Kulikova, A. Kondratyev, P. D. Round, D. Allen, C. R. Trainor, L. Gibson, and J. K. Szabo (2021). The State of Migratory Landbirds in the East Asian Flyway: Distributions, Threats, and Conservation Needs. Frontiers in Ecology and Evolution 9.

Yong, D. L., A. Jain, Y. Liu, M. Iqbal, C. Choi, N. J. Crockford, S. Millington, and J. Provencher (2018). Challenges and opportunities for transboundary conservation of migratory birds in the East Asian-Australasian flyway. Conservation Biology 32:740–743.

Yong, D. L., Y. Liu, B. W. Low, C. P. Española, C.-Y. Choi, and K. Kawakami (2015). Migratory songbirds in the East Asian-Australasian Flyway: a review from a conservation perspective. Bird Conservation International 25:1–37.

Youngflesh, C., J. Socolar, B. R. Amaral, A. Arab, R. P. Guralnick, A. H. Hurlbert, R. LaFrance, S. J. Mayor, D. A. W. Miller, and M. W. Tingley (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. Nature Ecology & Evolution 5:987–994.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney (2001). Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution 16:454–459.

Zenzal Jr., T. J., A. J. Contina, J. F. Kelly, and F. R. Moore (2018a). Temporal migration patterns between natal locations of ruby-throated hummingbirds (Archilochus colubris) and their Gulf Coast stopover site. Movement Ecology 6:2.

Zenzal Jr., T. J., D. Johnson, F. R. Moore, and Z. Németh (In Press). Environmental factors on the initiation of spring migration in four species of short- and medium-distance Nearctic songbird migrants. Journal of Avian Biology.

Zenzal Jr., T. J., F. R. Moore, R. H. Diehl, M. P. Ward, and J. L. Deppe (2018b). Migratory hummingbirds make their own rules: the decision to resume migration along a barrier. Animal Behaviour 137:215–224.

Zhao, X., M. Chen, Z. Wu, and Z. Wang (2014). Factors influencing phototaxis in nocturnal migrating birds. Zoological Science 31:781–728.

Zhou, Y., S. J. Smith, K. Zhao, M. Imhoff, A. Thomson, B. Bond-Lamberty, G. R. Asrar, X. Zhang, C. He, and C. D. Elvidge (2015). A global map of urban extent from nightlights. Environmental Research Letters 10:054011.

Zimmerman, J. K., J. Rojas-Sandoval, and A. B. Shiels (2021). Invasive Species in Puerto Rico: The View From El Yunque. Frontiers in Ecology and Evolution 9:640121.

Zimova, M., D. E. Willard, B. M. Winger, and B. C. Weeks (2021). Widespread shifts in bird migration phenology are decoupled from parallel shifts in morphology. Journal of Animal Ecology 90:2348–2361.

Zuckerberg, B., D. Fink, F. A. La Sorte, W. M. Hochachka, and S. Kelling (2016). Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. Diversity and Distributions 22:717–730.

Zurell, D., L. Gallien, C. H. Graham, and N. E. Zimmermann (2018). Do long-distance migratory birds track their niche through seasons? Journal of Biogeography 45:1459–1468.

Zurita-Milla, R., R. Goncalves, E. Izquierdo-Verdiguier, and F. O. Ostermann (2020). Exploring spring onset at continental scales: mapping phenoregions and correlating temperature and satellite-based phenometrics. IEEE Transactions on Big Data 6:583–593.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith (2009). Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY.

de Zwaan, D. R., A. Huang, Q. McCallum, K. Owen, M. Lamont, and W. Easton (2022). Mass gain and stopover dynamics among migrating songbirds are linked to seasonal, environmental, and life-history effects. Ornithology:ukac027.