Fire, Smoke, and Song: Impacts of fine particulate matter on the health, behavior, and detection of birds and other wildlife

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Abstract

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Birds are particularly vulnerable to air pollution, yet studies on the direct and indirect effects of air pollution on birds are limited. In this dissertation, I explored how fine particulate matter ($PM_{2.5}$) drives patterns in bird observations with the goal of providing insight into avian responses to air pollution and generating foundational knowledge to guide future study. I considered the effect of $PM_{2.5}$ in different contexts, both as a major component of wildfire smoke and as an urban air pollutant. I incorporated four distinct methods, including 1) executing a systematic literature review, 2) modeling the effect of $PM_{2.5}$ on the probability of observing birds, 3) evaluating the influence of $PM_{2.5}$ on birdsong and other soundscape features, and 4) using occupancy models to directly estimate the effect of $PM_{2.5}$ on detection of birds. Together, these approaches demonstrate spatial, temporal, and interspecific variation in the relationship

between $PM_{2.5}$ and bird observations and underscore the potential for interdisciplinary collaborations to rapidly advance research on the impacts of air pollution on birds.

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DEDICATION

To my cousins Anna and Julia Stevens, whose curiosity, creativity, and kindness provide an eternal source of joy and inspiration to me. To you and all the other young girls and women who love school and feel put down or counted out for daring to dream big, I offer this: Ignore the naysayers, for they do not know you, nor do their words determine your potential.

Chapter 1. INTRODUCTION

1.1 BACKGROUND

Over the last 50 years, the total number of birds in North America has declined by nearly 3 billion, which is equivalent to a 29% decrease in overall abundance (Rosenberg et al., 2019). Birds face numerous threats, including habitat loss due to climate change or land use change (Beaudry et al., 2013; Jetz et al., 2007; Schleupner & Link, 2008; Shaffer et al., 2019), poisoning from dietary exposure to pesticides (Hallmann et al., 2014; Hill et al., 1971; Wurster et al., 1965), collisions with buildings (Loss et al., 2014) and attacks by outdoor cats (Loss et al., 2013). Given the wide-ranging direct and indirect effects of air pollution on birds (Sanderfoot & Holloway, 2017), poor air quality might have also contributed to this population decline. In fact, a recent study showed that air pollution regulation designed to limit ambient concentrations of ozone directly contributed to the protection of 1.5 billion birds in the United States since 1980 (Liang et al., 2020). This finding suggests that the impact of air pollution on bird populations could be substantial. Yet, air quality is often overlooked in conservation biology and natural resource management (Leonard & Hochuli, 2017; Lovett et al., 2009), and there is still much to be learned about how birds and other wildlife are affected by inhalation exposure to airborne toxins (Smith et al., 2007).

Birds are particularly susceptible to adverse health outcomes associated with respiratory exposure to air pollution (Brown et al., 1997). Air pollution has been linked to immunosuppression (Wakabayashi et al. 1977, Lorz and López 1997, Olsgard et al. 2008, Cruz-Martinez et al. 2015a, Steyn and Maina 2015), respiratory illness (Morris et al., 1986; Simone-Freilicher, 2008; Verstappen & Dorrestein, 2005), elevated stress levels (Cruz-Martinez, Smits, et al., 2015), behavioral changes (Li et al., 2016; Sterner, 1993a, 1993b), and impaired reproductive success (Belskii et al., 1995, 2005; Eeva & Lehikoinen, 1995) in birds. However, most research to date on air pollution impacts on birds has either relied on a) data collected in controlled exposure experiments or b) field studies in which avian responses are compared within air pollution gradients or between more and less polluted study areas. While useful, both approaches are limited in advancing knowledge of air pollution impacts on wild, free-living birds and characterizing the sensitivity of avian responses to specific pollutants (Sanderfoot & Holloway, 2017). More research is needed to evaluate the direct and indirect effects of air pollution on birds, characterize dose-response relationships, and identify which species are most at risk. Studies linking ambient concentrations of reactive gases and aerosols to survival, growth, and reproductive rates in birds would be particularly useful, as these rates ultimately influence population trajectories. However, such studies are inherently challenging to design and costly to implement; furthermore, it is difficult to develop robust research objectives based on the limited number of studies currently available.

To advance this research agenda, I started by studying how air pollution influences detection of birds. Investigating how air quality drives patterns in bird observations is likely to provide key insight into avian responses to air pollution, as well as generate foundational knowledge to guide future research objectives. For example, we could find that detection of a particular species is negatively correlated with a specific air pollutant, or that the relationship between detection and air pollution varies in different habitats. I see this line of inquiry as a critical starting point to expand knowledge of air pollution impacts on birds — one that both provides information that is immediately useful for ornithologists and wildlife managers and also creates a springboard for further study.

1.2 RESEARCH OBJECTIVES

In my dissertation, I used four different approaches to explore the relationship between fine particulate matter ($PM_{2.5}$) and detection of birds, each of which is presented in a separate chapter. I focused on $PM_{2.5}$ because it is a ubiquitous, ground-level air pollutant that impacts communities around the world. Inhalation exposure to $PM_{2.5}$, which includes all suspended liquid and solid particles < 2.5 microns in aerodynamic diameter, is known to increase risk of adverse respiratory and cardiovascular health outcomes in humans (Anderson et al., 2012), and as such is regulated as a criteria air pollutant by the Environmental Protection Agency (EPA). There are both natural and anthropogenic sources of $PM_{2.5}$, and particles can be directly emitted or produced in chemical reactions. $PM_{2.5}$ is also a major component of wildfire smoke. As climate change intensifies wildfire activity (Abatzloglou & Williams, 2016; Westerling et al., 2011), it is increasingly important to consider the impact of large-scale smoke events and elevated concentrations of $PM_{2.5}$ on birds. In chapter two, I conducted a systematic literature review to synthesize research to date on the effects of wildfire smoke on the health and behavior of birds and other wildlife, with a particular emphasis on documenting measurements of air pollution during experiments and field studies. My goal was to establish a framework for linking shifts in observations of birds during wildfire smoke events to underlying health effects and behavioral responses. In chapter three, I used data from a large-scale citizen science program to model the effect of $PM_{2.5}$ on the probability of observing 71 bird species during the wildfire season in Washington state. This is the first study to directly link air pollution to detection of birds. In chapter four, I explored how $PM_{2.5}$ influenced diurnal variation in acoustic indices used to monitor birds and other wildlife. This study connects chapters two and three by investigating how $PM_{2.5}$ drives changes in a specific avian behavior, vocalization, which could ultimately affect detection of birds. In chapter five, I considered $PM_{2.5}$ as an urban air pollutant rather than a marker of wildfire smoke. In this study, I used occupancy models to evaluate the effect of $PM_{2.5}$ on detection of 46 bird species in urban and suburban areas in the Pacific Northwest during COVID-19 lockdowns.

1.3 BROADER IMPACTS

Together, these chapters demonstrate that wildfire smoke and urban air pollution influence detection of birds. In each chapter, I make specific recommendations for future studies and note opportunities and resources available to researchers. My dissertation emphasizes the value of connecting data on air quality and bird observations across varying spatial and temporal scales and emphasizes the need to establish interdisciplinary collaborations between ecologists and atmospheric chemists to rapidly advance knowledge of air pollution on birds. Future research on this topic will inform avian conservation, wildlife management, and environmental policy.

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Chapter 2. A REVIEW OF THE EFFECTS OF WILDFIRE SMOKE ON THE HEALTH AND BEHAVIOR OF WILDLIFE

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Abstract: Climate change is intensifying global wildfire activity, and people and wildlife are increasingly exposed to hazardous air pollution during large-scale smoke events. Although wildfire smoke is considered a growing risk to public health, few studies have investigated the impacts of wildfire smoke on wildlife, particularly among species that are vulnerable to smoke inhalation. In this review, we synthesized research to date on how wildfire smoke affects the health and behavior of wildlife. After executing a systematic search using Web of Science, we found only 41 relevant studies. We synthesized findings from this literature and incorporated knowledge gained from fields outside wildlife science, specifically veterinary medicine and air pollution toxicology. Although studies that directly investigated effects of smoke on wildlife were few in number, they show that wildfire smoke contributes to adverse acute and chronic health outcomes in wildlife and influences animal behavior. Our review demonstrates that smoke inhalation can lead to carbon monoxide poisoning, respiratory distress, neurological impairment, respiratory and cardiovascular disease, oxidative stress, and immunosuppression in wildlife, including terrestrial and aquatic species, and these health effects can contribute to changes in movement and vocalization. Some species also use smoke as a cue to engage in fire-avoidance behaviors or conserve energy. However, our review also highlights significant gaps in our understanding of the impacts of wildfire smoke on wildlife. Most notably, the lack of robust air pollution measurements in existing studies limits meta-analyses and hinders construction of dose-response relationships, thereby precluding predictions of health outcomes and behaviors under different air quality conditions, especially during extreme smoke events. We recommend that future studies leverage existing data sets, infrastructure, and tools to rapidly advance research on this important conservation topic and highlight the potential value of interdisciplinary collaborations between ecologists and atmospheric chemists. *Keywords:* Wildfires, smoke, air pollution, wildlife, monitoring, conservation, climate change

2.1 INTRODUCTION

As climate change intensifies the frequency and severity of wildfires, communities around the world are increasingly vulnerable to smoke pollution (Jacob & Winner, 2009). Increased wildfire activity has been linked to declines in average regional air quality and greater incidence of extreme air pollution episodes. For example, wildfires contributed to a recent increase in annual concentrations of fine particulate matter ($PM_{2.5}$, particles smaller than 2.5 microns in aerodynamic diameter) in the United States (Clay & Muller, 2019; McClure & Jaffe, 2018), and smoke events in the Pacific Northwest, United States in 2018 and 2020 caused $PM_{2.5}$ to spike to concentrations well above the National Ambient Air Quality Standards (NAAQS) (Liu et al., 2021; Washington State Academy of Sciences, 2019). Wildfire smoke directly contributes to adverse respiratory and cardiovascular health outcomes and mortality in humans (Chen et al. 2021; Cascio, 2018); in fact, studies have shown that the chemical composition of $PM_{2.5}$ in wildfire smoke is more toxic than that of urban ambient $PM_{2.5}$ (Aguilera et al., 2021; Franzi et al., 2011).

Wildfire smoke also sickens non-human animals, as illustrated by numerous case studies in veterinary medicine that document morbidity and mortality in domestic animals exposed to smoke, including pets and livestock (Fitzgerald & Flood, 2006; Marsh, 2007). These case studies demonstrate that, like people, animals can suffer from carbon monoxide poisoning, thermal and chemical damage to lung tissue, and greater susceptibility to respiratory disease as a result of smoke inhalation (Wohlsein et al., 2016). In fact, animal models, including mice, rats, rabbits, sheep, and monkeys, are often used to study the onset and progression of human disease following exposure to the toxic gases and aerosols found in smoke (David et al., 2009). Although many animals in fire-prone habitats are able to detect and avoid wildfires, fires still pose direct threats to wildlife (Engstrom, 2010; Nimmo et al., 2021), including exposure to extreme heat and smoke. Yet, the impacts of wildfire smoke on the health and behavior of wildlife are largely unknown (Erb et al., 2018; Geiser et al., 2018; Hovick et al., 2017; Lee et al., 2017).

This paucity of research on how wildfire smoke affects the health and behavior of wild animals hinders full consideration of the direct and indirect effects of wildfires when conducting risk assessments for wildlife and developing conservation plans. In addition, research on the impacts of wildfire smoke on wildlife is published in disparate journals spanning numerous disciplines (e.g., ecology, physiology, animal behavior, veterinary medicine, etc.); as such, ecologists, wildlife managers, and other stakeholders may be challenged to identify relevant studies. To date, review papers have synthesized findings on first-order effects of fire on animals, including injury, morbidity, and mortality (Engstrom, 2010), considered behavioral responses of mammals to fire, specifically torpor (Geiser et al., 2018), and discussed fire as an evolutionary force driving animal behavior and survival (Nimmo et al., 2021), but none have focused specifically on the effects of smoke from wildfires on the health and behavior of wildlife.

Wildfires are an important type of natural disturbance (Turner, 2010) in forests, grasslands, and deserts around the world, and many wildlife species benefit from resources available in post-fire landscapes (Smith, 2000). However, just as people now grapple with health risks posed by routine smoke events, even in airsheds where smoke pollution was previously uncommon (Wilmot et al., 2021), wildlife must also contend with greater — perhaps even novel — exposure to wildfire smoke with more intense wildfire activity. The magnitude of smoke events in the 21st century further underscores the urgent need to study the impacts of wildfire smoke on wildlife. Wildfire smoke persists in the atmosphere even after flames have subsided and can travel hundreds of miles, creating hazardous air quality conditions and degrading visibility across large geographic areas (Figure 2.1). As a result, smoke from a single wildfire could impact the health and behavior of wildlife at a much larger spatial scale than the area burned. Direct effects of wildfire smoke on individuals could scale to influence the demography of wildlife populations, with cascading community- and ecosystem-level impacts (Figure 2.2).

In this review, we synthesized research to date on the effects of wildfire smoke on the health and behavior of wildlife. We focused specifically on the impacts of wildfire smoke rather than describing all immediate effects of wildfires on wildlife in order to more deeply investigate physiological and behavioral responses of wildlife to the large-scale smoke events that are becoming increasingly common around the world. Below, we (1) identify relevant literature on the effects of wildfire smoke on the health and behavior of wildlife, (2) highlight knowledge gaps, and (3) present opportunities for rapidly advancing research on this important topic, all of which should serve as a useful resource for guiding ecological studies and conservation actions.

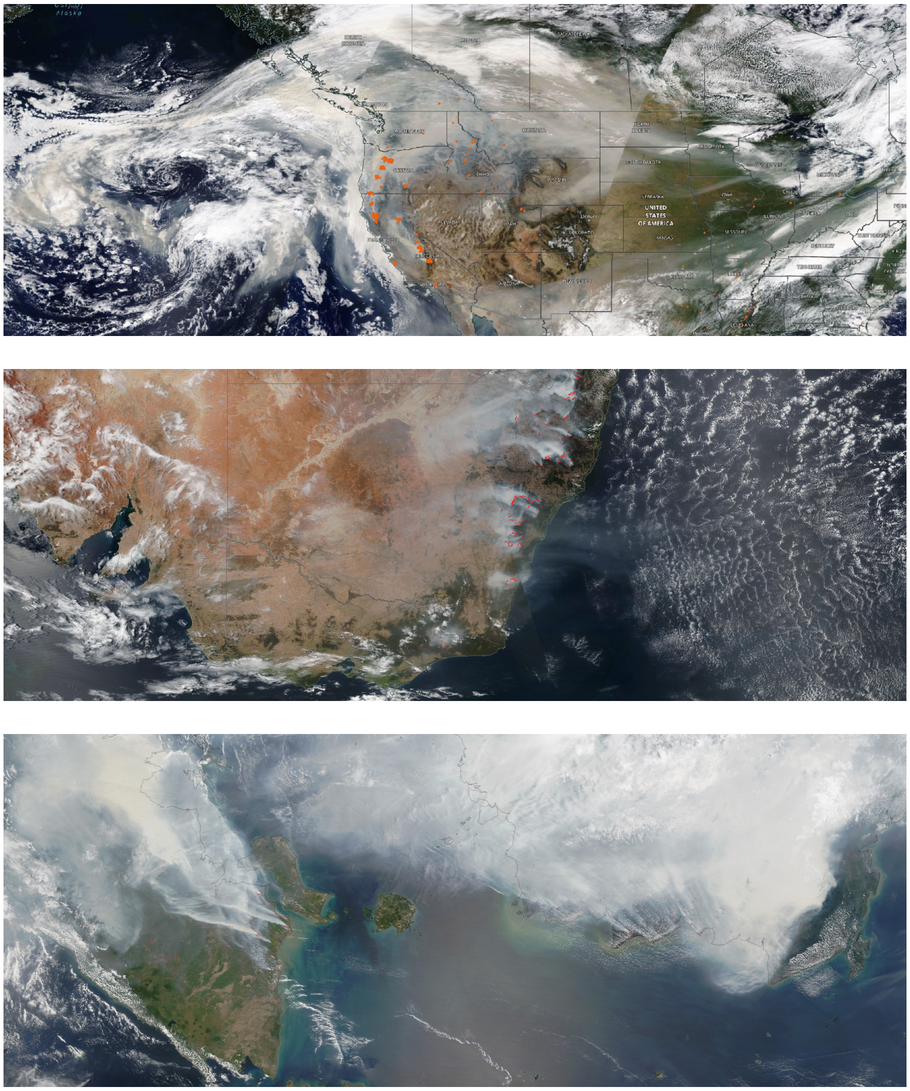


Figure 2.1: Satellite images of large-scale wildfire smoke events around the world. Orange points indicate locations of fires or thermal anomalies. *Top*: Smoke blows across the Western U.S. on September 13th, 2020. *Middle*: Wildfires in southeast Australia send up smoke plumes on December 17th, 2020. *Bottom*: Smoke blankets much of Indonesia on September 24th, 2015. Images downloaded from NASA Worldview at https://worldview.earthdata.nasa.gov/.

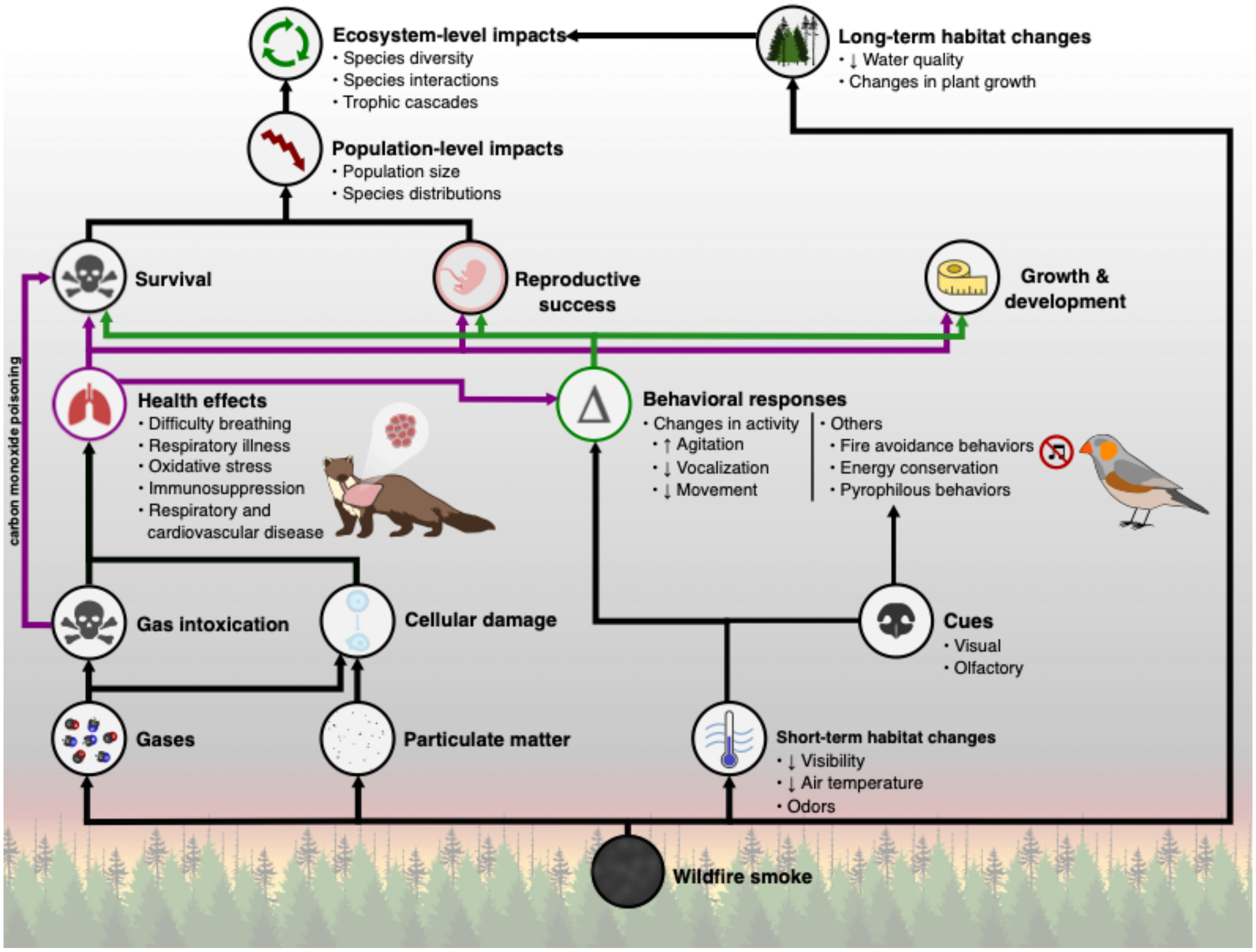


Figure 2.2: A conceptual model illustrating the various pathways by which wildfire smoke could influence wildlife populations and ecosystems. We hypothesize how effects of smoke on individual health and behavior could contribute to shifts in demographic rates, including growth and development, survival, and reproductive success. These parameters determine population growth, ultimately leading to community- and ecosystem-level impacts.

2.2 METHODS

In January 2021, we conducted two keyword searches using Web of Science (Figure 2.3). Search terms included 1) “wildfire* AND smoke*” and 2) “fire* AND smoke*”. We performed a basic search and entered search terms into the topic field. We excluded “news items” and “meeting abstracts” as document types to focus on peer-reviewed literature, then further refined our search results to include only articles from categories relevant to our review (e.g., environmental science, ecology, biology, physiology, toxicology, health sciences, veterinary sciences, etc.) A complete list of topic areas is provided in Appendix A.

We reviewed the titles of articles in both sets of search results (n = 4,314) (Figure 2.3). We earmarked articles with titles that included any of the following for further review: (1) the name of a specific domestic animal, wildlife species, or taxa (e.g., mammals, birds); (2) a general reference to animals or wildlife; (3) an example of an animal behavior (e.g., migration); or (4) an example of a health effect (e.g., mortality). We did not further review papers with titles suggestive of inquiry into ecosystem-level impacts of wildfires or the effects of fire or smoke on vegetation. We also excluded titles with clear references to human demographic groups (e.g., children) or epidemiological study (e.g., hospitals, emergency rooms). Next, we reviewed abstracts of articles earmarked in the review of titles (n = 295) to assess their eligibility for a full-text review (Figure 2.3). We assessed whether or not these papers presented research on the responses of animals to smoke from fires — regardless of the specific type of exposure investigated. Those that met these criteria were included in the list of papers that were read for this review (n = 72; Figure 2.3).

We sorted papers into three categories: (1) experiments using animal models; (2) case studies from veterinary medicine; and (3) research on the effects of smoke on wildlife species (Figure 2.3). For the last category, we considered “wildlife” to include all non-domesticated fauna in terrestrial environments, including insects, as well as aquatic animals that breathe air, such as marine mammals. This allowed us to focus on the direct effects of smoke on wildlife, rather than explore all possible indirect effects that could arise from atmospheric deposition of airborne toxins found in wildfire smoke. At least one of the co-authors of this review read and documented findings from studies of animal models (n = 36) and case studies from veterinary medicine (n = 18). However, we focused our review on studies of the impacts of smoke on wildlife (n = 18). At least two co-authors of this review read and documented findings from each of these papers. In addition, we used Web of Science to conduct forwards searches, noting any citations of these studies that referenced all of the following in the title: (1) smoke, or more generally air pollution associated with fires; (2) animals, wildlife, or the name of a particular species or taxa; and (3) an animal behavior or health effect. We also conducted backwards searches using two different approaches: (1) we noted citations that may be relevant to our review while reading a paper, and (2) we conducted a backwards search of all works cited in the paper using the same criteria described for the forwards search. All additional studies on the effects of smoke on wildlife species identified in forwards and backwards searches were also reviewed (n = 16) (Figure 2.3). In addition to noting major findings from these papers, we pulled out several key pieces of information to characterize the research and compare results across studies, including publication year, field of study, location, type of exposure, concentrations of air pollutants (if provided), and taxa and species of animals studied, as well as whether the animals were captive (i.e., kept in a laboratory or outdoor enclosure), or free-living (i.e., in the wild). Finally, we noted whether the ultimate goal of the study was to investigate effects of smoke in people or non-human animals. While preparing this manuscript, we learned of 7 additional studies that considered the impacts of wildfire smoke on wildlife, which we also included in our review. Although we did not restrict our initial keyword searches in Web of Science by language, each subsequent step of our review was limited to text available in English. In addition, we were only able to review articles available through the University of Washington library system. All together, we reviewed 41 studies that considered the effects of wildfire smoke on wildlife (Figure 2.3, Table 2.1).

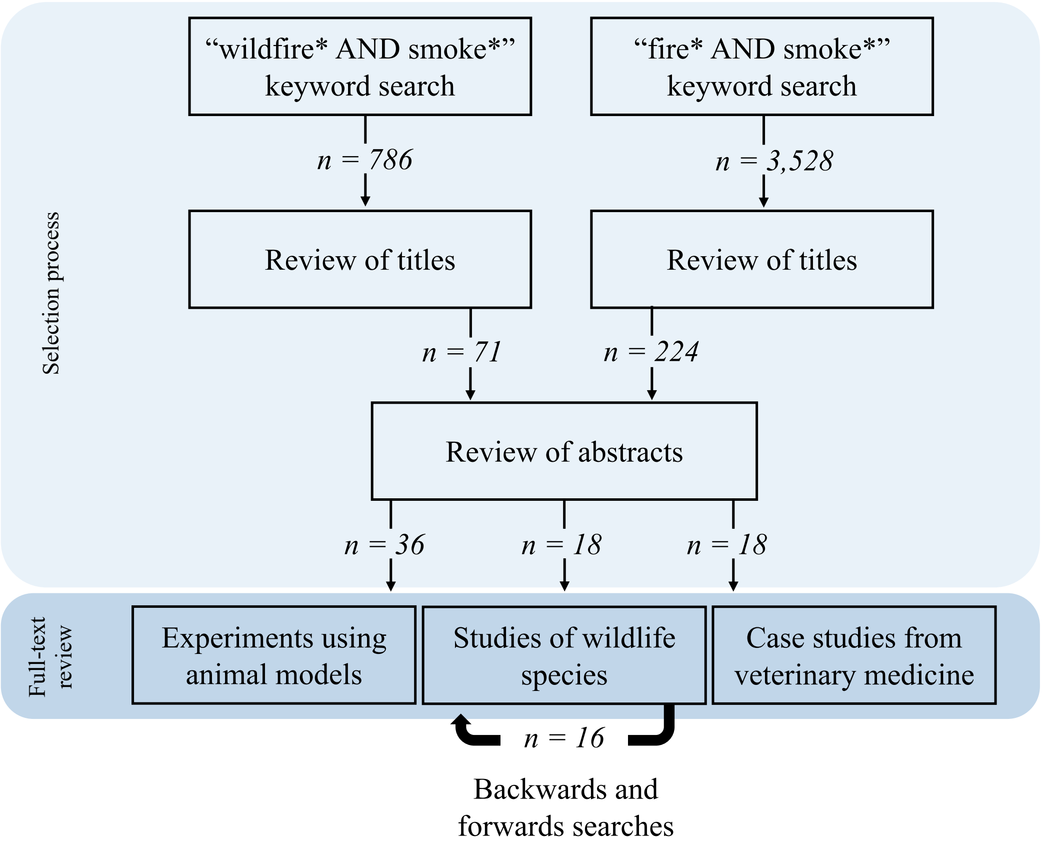
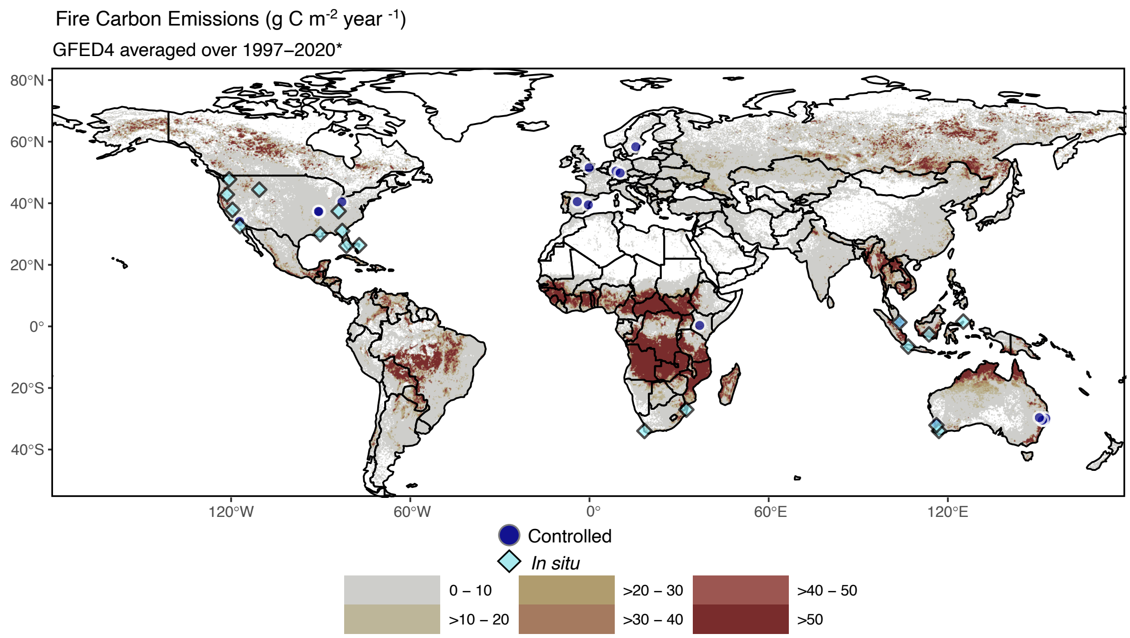


Figure 2.3: A schematic illustration of methods used to identify literature included in our review. We show steps in chronological order, starting at the top and working down. Our initial keyword searches yielded 4,314 titles, of which we found 295 were relevant based on a review of titles. After reviewing abstracts of these papers, we identified 72 that we thought merited a full-text review. We sorted these papers into three categories: experiments using animal models, case studies from veterinary medicine, and studies of wildlife species. We conducted backwards and forwards searches on papers specific to wildlife and included all studies of wildlife species in our review.

2.3 RESULTS

We found that although research to date on the impacts of wildfire smoke on wildlife is limited, existing evidence suggests that smoke pollution has wide-ranging direct and indirect effects on both terrestrial and aquatic wildlife. Studies have linked smoke inhalation to acute and chronic health outcomes in animals and sought to characterize how smoke influences animal behavior. Whereas the designs of these studies are highly variable, two general approaches have emerged in the literature: (1) experiments in which animals were intentionally exposed to smoke or constituents of smoke in a controlled environment (i.e., "controlled exposure") and (2) opportunistic monitoring of free-living animals or animals in captivity during wildfire smoke events (i.e., "*in situ* exposure"). The studies we reviewed were conducted on five continents, including North America, Australia, Europe, Asia, and Africa (Figure 2.4), and published between 1968 and 2021. They explored responses in a wide variety of taxa, including mammals, birds, reptiles, and insects in both controlled and *in situ* settings (Figure 2.5). A complete list of studies reviewed is provided in Table 2.1. In sections 4 through 6, we detail findings from this literature while also incorporating knowledge gained from fields outside wildlife science, specifically veterinary medicine and air pollution toxicology. Finally, in section 7, we briefly summarize studies of indirect effects of smoke on wildlife and consider how a species' life-history strategy mediates its exposure to smoke pollution.



* Estimates from 2017 to 2020 were derived from the relationship between active fires and emissions.

Figure 2.4: A map of global carbon (C) emissions, measured in g C/m^2/year, marked with the locations of the 36 controlled exposure experiments and *in situ* studies included in our review. We reviewed five additional studies that were not matched to a specific study location. Dark blue circles indicate locations of controlled exposure experiments and light blue triangles indicate locations of *in situ* studies. The limited overlap between study locations and emissions demonstrates that there are several regions likely exposed to large-scale smoke events where few studies have been conducted on the effects of wildfire smoke on the health or behavior of wildlife. Data on fire emissions is available from the Global Fire Emissions Database (GFED4) at https://www.globalfiredata.org/data.html (Giglio et al., 2013).

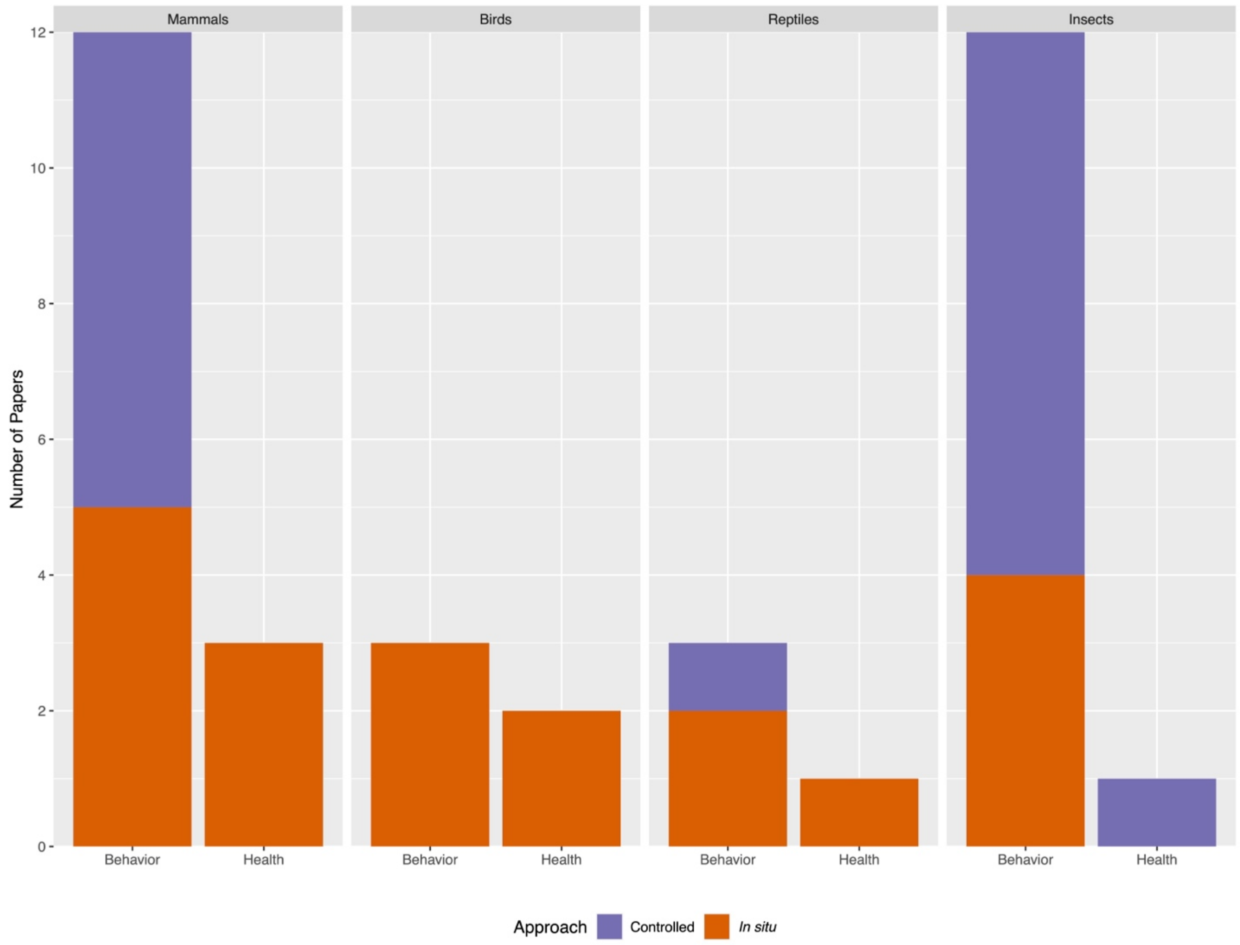


Figure 2.5: Distribution of studies that considered how wildfire smoke impacts the health and/or behavior of wildlife. Each column represents the number of papers we found on health effects or behavioral responses for a specific taxon, broken down by research approach (i.e., controlled exposure or *in situ* exposure). Some papers investigated both health effects and behavioral responses or considered multiple taxa and are therefore counted more than once. We did not find any papers on direct effects of wildfire smoke on amphibians.

2.4 ACUTE AND CHRONIC HEALTH OUTCOMES

Few studies have explicitly considered the impact of wildfire smoke on the health of wildlife (Table 2.1); however, research from veterinary medicine and air pollution toxicology clearly demonstrates that smoke inhalation contributes to acute and chronic health outcomes in animals. Case studies detailing the symptoms, treatment, and recovery of pets and livestock following structural fires establish that animals are vulnerable to negative health outcomes from smoke inhalation (e.g., Drobatz et al., 1999a, 1999b; Marsh, 2007). In addition, there are numerous examples of laboratory experiments designed to investigate the effects of inhalation exposure to wildfire smoke in humans using animal models (e.g., Hargrove et al., 2019; Martin et al., 2020) including mice, rats, rabbits, and sheep. Although the objective of these studies is to characterize the underlying physiological mechanisms that contribute to respiratory disease in humans, their findings allude to health effects we could observe in other mammalian species. These experiments have incorporated *in vivo*, *ex vivo*, and/or *in vitro* approaches. Some studies have also used animal models to study possible treatment interventions to improve health outcomes in humans following smoke inhalation (e.g., Dunn et al., 2018; Hamahata et al., 2008; Janssens et al., 1994; Wang et al., 1999; Syrkina et al., 2007; Wong et al., 2004).

Research has largely focused on mammals, but all animals that breathe air — whether terrestrial or aquatic — are vulnerable to inhalation exposure to airborne toxins, including the reactive gases and aerosols that make up smoke (e.g., carbon monoxide (CO), hydrogen cyanide (HCN), and coarse and fine particulate matter (PM)). Many animals are susceptible to CO poisoning during smoke inhalation (Ashbaugh et al., 2012; Bidani et al., 1998; Chaturvedi et al., 1995; Dörfelt et al., 2014; Fitzgerald & Flood, 2006; Kent et al., 2010; Stern et al., 2014), which can be fatal (Wohlsein et al., 2016). CO binds to hemoglobin, a protein molecule containing iron that nearly all vertebrates (Ruud, 1954) and many invertebrates depend on to carry oxygen through the bloodstream. This limits oxygen transport, resulting in low blood oxygen levels (i.e., hypoxemia) and insufficient supply of oxygen to tissues and organs (i.e., hypoxia) (Dubick et al., 2002; Lange et al., 2014; Wohlsein et al., 2016). Neurological symptoms of hypoxic brain damage could include confusion and stupor (Drobatz et al., 1999a, 1999b; Guillaumin & Hopper, 2013; Kent et al., 2010; Mariani, 2003; Weiss et al., 2011). Hypoxia could also make animals more vulnerable to predation as they attempt to flee wildfires (Braithwaite & Estbergs, 1987).

Smoke inhalation also causes both thermal and chemical damage to lung tissue in terrestrial and aquatic vertebrates (Fitzgerald & Flood, 2006; Marsh, 2007; Wohlsein et al., 2016). As a result of this injury, fluid can accumulate in the lungs, a condition known as pulmonary edema (Bidani et al., 1998; Jordaan et al., 2020), which has been documented in pets and livestock exposed to smoke during structural fires (Fitzgerald & Flood, 2006; Marsh, 2007; Verstappen & Dorrestein, 2005). Symptoms of smoke inhalation injury can be immediate or delayed and include labored breathing (i.e., dyspnea) (Verstappen & Dorrestein, 2005), rapid breathing (i.e., tachypnea) (Mariani, 2003), wheezing, panting (i.e., polypnea) (Dörfelt et al., 2014; Verstappen & Dorrestein, 2005), coughing (Dörfelt et al., 2014; Fitzgerald & Flood, 2006; Kemper et al., 1993), foaming at the nostrils (McPherson, 1993; Wohlsein et al., 2016), hypothermia, and rapid heart rate (i.e., tachycardia) (Dörfelt et al., 2014), which are consistent with acute respiratory distress syndrome (Dörfelt et al., 2014; Drobatz et al., 1999b; Guillaumin & Hopper, 2013; Kemper et al., 1993; Verstappen & Dorrestein, 2005). If untreated, smoke inhalation injury can quickly impair gas exchange, resulting in hypoxemia (Hamahata et al., 2008; Lange et al., 2014) and elevated levels of acid in the blood (i.e., acidosis) (Bidani et al., 1998). For example, in a retrospective analysis of health records of captive bottlenose dolphins (*Tursiops truncatus*), researchers found that blood carbon dioxide (CO_2) levels were elevated in the month following a wildfire smoke event in 2003, possibly due to respiratory acidosis (Venn-Watson et al., 2013). Air-breathing invertebrates might also be vulnerable to smoke inhalation. Tan et al. (2018) investigated effects of smoke exposure in captive squinty bush brown butterflies (*Bicyclus anynana*) and found that particles accumulated in the entryway of spiracles

— external openings in the exoskeleton that vent the insect respiratory system — but did not enter the trachea.

Wildfire smoke contributes to chronic respiratory and cardiovascular health outcomes in animals. Smoke inhalation can jeopardize an animal's immune system, which is designed to protect the body from foreign matter, such as bacteria, viruses, and toxins. In mammals, smoke inhalation immediately triggers production of immune cells, including lymphocytes (e.g., T cells) and macrophages (Barrett et al., 2006; Bidani et al., 1998; Hamahata et al., 2008; Hargrove et al., 2019; Syrkina et al., 2007) — a type of white blood cell that engulfs and digests (i.e., phagocytizes) foreign particles. However, exposure to wildfire smoke can alter (Venn-Watson et al., 2013) or weaken (Black et al., 2017) the immune response in animals. For example, whereas macrophages are able to sequester toxic particles in wildfire smoke, they are unable to destroy them; this precludes macrophages from helping to prevent infection (Wohlsein et al., 2016). Furthermore, toxins in smoke also destroy antioxidants, substances that neutralize free radicals — highly reactive, oxygen-containing compounds that damage tissue (Hamahata et al., 2008; Shalini et al., 1994; Wegesser et al., 2010). Oxidative stress can ultimately contribute to compromised immune function by destroying macrophages or other types of immune cells (Franzi et al., 2011; Williams et al., 2013). Lung injury and a weakened immune response (Matthew et al., 2001) can leave animals more vulnerable to respiratory infection and illness, such as pneumonia (Attwood et al., 1996a, 1996b; Guillaumin & Hopper, 2013; Marsh, 2007; Matthew et al., 2001; Simone-Freilicher, 2008; Verstappen & Dorrestein, 2005; Wohlsein et al., 2016) or laryngotracheitis (Morris et al., 1986). For example, captive bottlenose dolphins were three times more likely to have bacterial pneumonia at time of death after exposure to smoke during a wildfire in 2003 (Venn-Watson et al., 2013). However, age also influenced the incidence of pneumonia, and after controlling for age, the effect of fires was no longer statistically significant (Venn-Watson et al., 2013). A study of rhesus macaque monkeys (*Macaca mulatta*) housed in outdoor enclosures found that newborn monkeys exposed to wildfire smoke exhibited reduced lung capacity and weakened immune responses in adolescence compared to those born in a subsequent year with good air quality (Black et al., 2017). Whereas this study was designed to investigate pediatric health outcomes in humans associated with wildfire smoke, these results suggest that wildlife could experience long-term, adverse health outcomes from a single smoke event. Smoke inhalation can also impair cardiovascular function in vertebrates (Kim et al., 2014; Sharpe et al., 2020; Thompson et al., 2018; Wohlsein et al., 2016) and repeated or prolonged exposure to smoke can lead to chronic heart disease (Martin et al., 2020; Thompson et al., 2018).

Health outcomes associated with inhalation of wildfire smoke vary as a function of its toxicity. Research from air pollution toxicology demonstrates that toxicity of biomass smoke is dependent on its chemical and biological composition (Franzi et al., 2011; Kim et al., 2019), which is determined by the substrate burned (e.g., peat, oak, eucalyptus, etc.) and combustion conditions (e.g., flaming, smoldering) (Hargrove et al., 2019; Kim et al., 2019). Smoke is also subject to chemical transformation during long-range transport (Jalava et al., 2006). This suggests that the specific types of vegetation burned during wildfires, the stage and severity of the fires, and the distance smoke travels ultimately affect respiratory and cardiovascular health outcomes associated with smoke inhalation in wildlife.

2.5 IMPACTS ON DEMOGRAPHY

Negative health outcomes associated with inhalation exposure to wildfire smoke could ultimately influence demographic rates in wildlife populations, including survival, growth, and reproductive success (Figure 2.2). *In vivo* studies of animal models (e.g., Bidani et al., 1998; Dubick et al., 2002; Lee et al., 2005; Matthew et al., 2001; Syrkina et al., 2007) and case studies from veterinary medicine (e.g., Dörfelt et al., 2014; Drobatz et al., 1999b; Kent et al., 2010; Morris et al., 1986; Stern et al., 2014) provide clear evidence that animals can die from smoke inhalation. For example, Anderson et al. (2020) linked elevated concentrations of $PM_{2.5}$ during a large-scale smoke event to increased mortality in dairy cows, specifically calves. Yet, we found only four studies that considered the effect of smoke on survival of wildlife species. A study of captive butterflies reared in smoky conditions found that caterpillars exposed to smoke exhibited a higher mortality rate than those in the control group, likely due to gas intoxication (Tan et al., 2018). Gas intoxication was also hypothesized as a contributing factor to the death of lizards and snakes that did not survive prescribed burns in Tembe Elephant Park, South Africa (Jordaan et al., 2020). Few specimens exhibited signs of burn injury, yet Jordaan et al. found that 61% of specimens collected at the site of one fire exhibited pulmonary edema and noted particles accumulated in the lungs of two of these specimens. These findings suggest that reptiles that did not survive the fire died from asphyxiation, CO or HCN poisoning, or heat-induced cardiac arrest. Large mammals are also vulnerable to smoke inhalation — Singer et al. (1989) reported that smoke inhalation injury or gas intoxication likely killed 246 elk (*Cervus elaphus*) that perished in the 1988 wildfires in Yellowstone National Park. Finally, Yang et al. (2021) found that smoke from extensive wildfires in the Western U.S. contributed to a mass avian mortality event in 2020.

Wildfire smoke could also reduce growth rates and reproductive success. Tan et al. (2018) reported that captive squinty bush browns exposed to smoke developed more slowly and weighed less as pupae. Cahill & Walker (2000) reported that the nesting success of Red-knobbed

Hornbills (*Aceros cassidix*) declined at the Tangkoko Nature Reserve in Indonesia following extensive wildfires in 1997, possibly due to exposure to extreme heat and smoke. Although the Red-knobbed Hornbill example was the only study we found that considered the impacts of wildfire smoke on reproductive success in wild animals, a case study of domestic chickens exposed to smoke during a structural fire suggests that smoke inhalation could reduce egg production (Morris et al., 1986). Previous research has linked other types of air pollution to reduced hatching success and lower clutch size in birds (e.g., Eeva & Lehikoinen, 1995), which suggests that wildfire smoke could also impair avian reproductive success. In addition, PM — a major component of wildfire smoke — dirties bird feathers, which can render them less attractive to potential mates (Griggio et al., 2011) and interfere with other color-based signaling or camouflage.

2.6 BEHAVIORAL RESPONSES

Wildfire smoke can also trigger shifts in animal behavior, including movement and vocalization. Such behavioral changes could be due to underlying health effects (Erb et al., 2018) or serve to limit exposure to airborne toxins (Dickinson et al., 2009; Liu et al., 2021; Singer et al., 1989). Some species rely on smoke as an early-warning signal that helps them to avoid wildfires (Álvarez-Ruiz et al., 2021; Engstrom, 2010; Höcherl & Tautz, 2015) or prepare to conserve energy in a post-fire landscape (Geiser et al., 2018), whereas others use smoke as a cue to navigate toward newly available resources in burned habitats (Klocke et al., 2011; Milberg et al., 2015; Schütz et al., 1999). Animals could also change their behavior in response to alterations in the physical environment that result from smoke pollution (Cheyne, 2008; Lee et al., 2017), such as reduced visibility (Haider et al., 2019) or cooler air temperatures (Robock, 1991). Emerging evidence suggests that behavioral responses to wildfire smoke could ultimately influence the short- and long-term fitness of wildlife (Cheyne, 2008; Erb et al., 2018).

2.6.1 *Effects of Smoke on Wildlife Activity*

Exposure to smoke can influence wildlife activity, including movement and vocalization. Case studies from veterinary medicine demonstrate that animals sometimes alter their behavior due to acute, adverse health effects associated with smoke inhalation; for example, pets and livestock exposed to smoke from structural fires can become agitated, (Fitzgerald & Flood, 2006; Guillaumin & Hopper, 2013; Marsh, 2007; Mendyk et al., 2020; Weiss et al., 2011), vocalize more (Fitzgerald & Flood, 2006; Weiss et al., 2011), reduce their activity (Simone-Freilicher, 2008) or exhibit signs of neurological impairment, such as disorientation (Guillaumin & Hopper, 2013; Marsh, 2007; Weiss et al., 2011). Researchers observed that pinecone lizards (*Tiliqua rugosa*) in captivity exhibited rapid tongue-flicking when exposed to smoke near their enclosure, a sign of agitation (Mendyk et al., 2020). Animals in the wild could also alter their behavior in response to smoke pollution, possibly due to underlying health effects, as noted in one of the only studies to directly link wildfire smoke exposure to specific health outcomes for a wildlife species (Erb et al., 2018). In this study, researchers documented the daily activity of male Bornean orangutans (*Pongo pygmaeus wurmbii*) before, during, and after an extensive wildfire smoke event in Indonesia. They also collected urine samples opportunistically to test for ketones, a marker of fat catabolism associated with energy expenditure. The researchers found that orangutans rested more both during and after the smoke event. Furthermore, after the smoke event, orangutans traveled shorter distances and increased their caloric intake, but expended more energy (i.e., increased fat catabolism). Despite conserving energy and eating more food, orangutans still burned more calories than they consumed after an extended period of smoke exposure, which suggests that smoke inhalation negatively affected their energy budgets. The researchers postulated this could have been due to stress or a heightened immune response (Erb et al., 2018).

In addition to movement, smoke can also influence animal vocalization. For example, a study of singing behavior in Bornean white-bearded gibbons (*Hylobates albibarbis*) in Indonesia found that gibbons sang less when it was smoky — during months when wildfire smoke led to unhealthy air quality, both the number of days gibbons sang and the length of singing bout decreased (Cheyne, 2008). Changes in vocalization during wildfire smoke events may ultimately influence entire soundscapes (Lee et al., 2017). An analysis of audio recordings collected in Singapore during a haze event brought on by wildfires showed that wildlife acoustic activity, as measured by four acoustic indices, was negatively correlated with smoke pollution. Although the mechanisms driving this response were beyond the scope of the study, its authors hypothesized that several factors could have contributed to a decrease in acoustic activity, including reduced vocalization, a shift in ecological activity outside the recording period, or mortality due to direct effects of smoke exposure or reduced foraging success. Acoustic activity was suppressed for months following the smoke event, illustrating that smoke could have long-term impacts on species and communities (Lee et al., 2017).

2.6.2 *Use of Smoke as a Cue*

2.6.2.1 Fire-avoidance Behaviors

Wildlife across taxa, including insects, reptiles, and mammals, rely on smoke as a cue to engage in fire avoidance behaviors (Nimmo et al., 2021). Insects may relocate after detecting smoke to evade fires. Researchers in Germany exposed European paper wasps (*Polistes dominula*) to biomass smoke and found that the insects increased their thorax temperature in response to this stressor (Höcherl & Tautz, 2015). Many insects must warm up their thoraces before flying; as such, the results of this experiment suggest that smoke prompts a pre-flight warm-up behavior in wasps that prepares them for a quick escape from nearby fire (Höcherl & Tautz, 2015). Researchers exposed ants in Kenya to smoke generated by burning elephant dung and found that two of the four study species evacuated in response to smoke, relocating up to 1,800 meters (Sensenig et al., 2017). Of the two ant species that responded to smoke, the subordinate ant species (*Crematogaster nigriceps*) evacuated twice as quickly as the dominant competitor (*C. mimosae*). These results suggest that subordinate species may be more willing to adopt a colonist strategy following disturbance and therefore are better equipped to escape and survive wildfires (Sensenig et al., 2017). However, some insects, such as the Cape honeybee (*Apis mellifera capensis*), may not attempt to evade fire and instead use smoke as a cue to retreat to protective nest structures (Tribe et al., 2017). Regardless of their fire avoidance strategy, smoke could compromise the ability of insects to escape fires by impairing flight performance (Liu et al., 2021). Liu et al. (2021) found that the duration, distance, and speed flown by painted lady butterflies (*Vanessa cardui* L.) decreased following exposure to smoke, which could adversely impact other insect behaviors as well, such as foraging and migration (Liu et al., 2021).

Studies of captive lizards suggest that smoke can also trigger fire avoidance behaviors in reptiles (Álvarez-Ruiz et al., 2021; Mendyk et al., 2020). For example, captive Psammodromus lizards (*Psammodromus algirus*) exhibited a variety of escape behaviors when exposed to smoke, including running and scratching at their terrariums (Álvarez-Ruiz et al., 2021). Furthermore, lizards were more likely to increase their activity in response to smoke if they were captured in habitats prone to wildfires, regardless of an individual's previous experience with fire. These results indicate that in areas that experience frequent fires, selective pressure drives greater sensitivity to smoke, increasing the ability of local populations to detect and evade fires (Álvarez-Ruiz et al., 2021).

Smoke can also prompt mammals to arouse from torpor, enabling them to escape fires (Doty et al., 2018; Layne, 2009; Nowack et al., 2016; Scesny, 2006; Stawski et al., 2015). However, not all torpid mammals flee in response to smoke, or react quickly enough to survive; responses to fire stimuli are likely to vary by species, sex, and individual (Layne, 2009; Nowack et al., 2016, 2018). In addition, lower ambient temperatures slow torpor arousal following smoke exposure, which suggests that torpid mammals are less able to evade fires on colder days (Doty et al., 2018; Layne, 2009; Nowack et al., 2016). Furthermore, animals that detect smoke and arouse from torpor at cooler temperatures might not return to steady-state torpor, which increases their energy expenditure (Doty et al., 2018).

To avoid fires, small animals might seek shelter underground or in rock crevices (Engstrom, 2010); however, burrowing may not always protect animals from extreme heat and smoke. For example, Jordaan et al. (2020) noted that fossorial species were well-represented in their samples of dead reptile specimens collected after prescribed burns in Tembe Elephant Park, South Africa. They hypothesized that cause of death was likely asphyxiation, gas intoxication, or heat-induced cardiac arrest, which suggests that even burrowing animals are susceptible to smoke inhalation during fires (Jordaan et al., 2020).

2.6.2.2 Energy-saving Behaviors

Some animals rely on smoke as an indicator of impending food scarcity, prompting them to engage in energy-saving strategies. Small mammals must maintain high metabolic rates, which is difficult after fires due to limited availability of food and water. Studies of captive small mammals show that smoke can increase use of torpor in some species, allowing animals to conserve energy and survive post-fire conditions (Geiser et al., 2018). For example, exposure to smoke and a substrate of charcoal and ash increased duration of torpor in captive yellow-footed antechinuses (*Antechinus flavipes*) (Stawski et al., 2017) and captive sugar gliders (*Petaurus breviceps*) (Nowack et al., 2018). However, use of torpor after fires depends on food availability, and is likely to vary by species (Nowack et al., 2018) and sex (Stawski et al., 2017).

2.6.2.3 Resource Availability

Pyrophilous insects (i.e., fire-associated species that benefit from resources available in post-fire landscapes) can use smoke as a cue to navigate toward fires, responding to thermal and/or olfactory signals (Álvarez et al., 2015; Klocke et al., 2011; Milberg et al., 2015; Schütz et al., 1999). Some are even known to swarm in smoke plumes, such as "smoke flies" of the genera Microsania and Hormopeza, possibly to mate near burned trees where they deposit their eggs (Evans, 1966; Sinclair & Cumming, 2006; Snoddy & Tippins, 1968). Schütz et al. (1999) found that the antennae of fire bugs (*Melanophila acuminata*) respond to volatiles generated in the combustion of pine, suggesting that the smell of smoke helps some beetles detect and locate burned trees. Insects may also respond to visual cues of smoke plumes but results from experimental studies are ambiguous (Hinz et al., 2018). An influx of aerial insects to burned habitats could enhance foraging opportunities for bats (de Torrez et al., 2018) and insectivorous birds; unlike small, quadrupedal mammals, bats might actually decrease their use of torpor after fires to take advantage of this increase in food availability (Geiser et al., 2018). Raptors may also be attracted to smoke plumes, which could signal an opportunity to prey on insects and small mammals fleeing fire (Hovick et al., 2017).

Whereas pyrophilous insects appear to rely on olfaction to locate burned areas, exposure to smoke can impair detection of other scents. Visscher et al. (1995) found that the antennae of honey bees (*Apis mellifera*) exposed to smoke were less responsive to both a floral odor and alarm pheromones. This suggests that detection of smoke could have short-term impacts on foraging and defensive behaviors in insects (Visscher et al., 1995).

2.7 EFFECTS ON WILDLIFE HABITAT

Several studies have sought to quantify potential exposure to smoke for species that use specific habitats, although they did not evaluate the impact of smoke on animal health or behavior (e.g., Bova et al., 2011; O'Brien et al., 2006; Thompson & Purcell, 2016). O'Brien et al. (2006) measured air quality in a hole that could be used as a nesting cavity by Cuban parrots (*Amazona leucocephala*) during a prescribed burn. They found that as flames passed the cavity entrance, smoke accumulated inside for about 20 minutes, and CO_2 concentrations sharply increased to 2,092 parts per million (ppm). O'Brien et al. (2006) described these conditions as "benign," but pointed to the lack of research to date on inhalation exposure to air pollution in birds. Thompson & Purcell (2016) took a similar approach to assess the vulnerability of fishers (*Pekania pennanti*) to smoke during prescribed burns, measuring the concentration of CO in tree cavities that were previously used or could be used as den sites. They found that whereas levels of CO during burns might not be harmful to adult fishers, they are hazardous to developing fetuses and newborns. Dickinson et al. (2010) used air quality data collected during prescribed burns to determine if smoke exposure endangered Indiana bats (*Myotis sodalis*). They determined that CO concentrations during low-intensity prescribed burns were unlikely to be dangerous but suggested that bats that roost in foliage or under bark could be more vulnerable to gas intoxication during fires than bats that roost in cavities or crevices where concentrations of poisonous gases are lower (Dickinson et al., 2010). Dickinson et al. (2009) found that CO concentrations during a prescribed burn did not exceed the threshold at which incapacitation of bats would likely occur; however, they noted that bats that roost closer to the ground would be more at risk of exposure to elevated concentrations of toxic gases. Cave-roosting bats in particular could be in danger of smoke inhalation because caves could fill with smoke before bats have a chance to escape (Dickinson et al., 2009; Geiser et al., 2018). These findings illustrate that exposure to air pollution during wildfires varies widely, depending on the specific habitats used by wildlife.

Although we primarily focused our review on the direct effects of wildfire smoke on the health and behavior of wildlife, it is worth considering how smoke pollution indirectly affects wildlife by driving short-term changes in habitat. Smoke limits visibility (Haider et al., 2019) and cools air temperatures (Robock, 1991) — changes in the physical environment that could influence the health and behavior of wild animals. While vegetative succession following wildfires generates habitat for a wide variety of fauna (Jones & Tingley, 2021; Smith, 2000; Stillman et al., 2021), smoke *from* wildfires also has immediate impacts on plant growth. For example, wildfire smoke triggers seed germination in plants that grow in fire-prone habitats (van Staden et al., 2000). Smoke can also positively or negatively influence plant productivity, depending on the extent to which aerosols absorb or scatter sunlight, as well as ambient concentrations of co-pollutants that damage plants (Hemes et al., 2020). Furthermore, pollutants in smoke can deposit on soils or vegetation, which can indirectly affect wildlife (Phaneuf et al., 1995). Plants can absorb toxins in smoke that, if consumed, could compromise the health of herbivorous animals (Tan et al., 2018). Wildfire smoke also affects aquatic habitats (Jaafar & Loh, 2014). Smoke limits how far light penetrates underwater, which can influence the vertical distribution of microorganisms (Urmy et al., 2016) or primary productivity of coral reefs (Risk et al., 2003). Atmospheric deposition of aerosols in smoke can also degrade water quality (Corbin, 2012; Earl & Blinn, 2003; Phaneuf et al., 1995), which can in turn alter the composition of macroinvertebrate communities (Earl & Blinn, 2003) and negatively affect the health of fish or other water-breathing animals (Gonino et al., 2019; Gresswell, 1999).

Table 2.1: Summary of studies of wildlife species included in our review. For each paper, we provided the in-text citation, broad taxonomic category and specific species studied, and type of exposure (i.e., *in situ* or controlled) investigated. We also indicated whether a study assessed impacts in captive or free-living animals. In addition, we included the location and continent where each study took place. If locations for studies of captive animals were not provided, we noted the location of the research institution of the first author. We also provided a description of smoke exposure. Finally, we indicated if a health outcome and/or a behavioral response was observed. Citations are listed in alphabetical order.

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Álvarez et al. 2015	Insects	Pine sawyer (*Monochamus galloprovincialis*)	Controlled (excised antennae)	Insects captured in Valencia, Spain. Experiment conducted in Palencia, Spain.	Europe	Excised antennae exposed to six smoke volatiles.	No	Yes
Álvarez-Ruiz et al. 2021	Reptiles	Large psammodromus (*Psammodromus algirus*)	Controlled (captive)	Lizards captured on the eastern Iberian Peninsula in Spain. Study conducted in Valencia, Spain.	Europe	Smoke generated from burning pine.	No	Yes
Bova et al. 2011	Birds	Red-cockaded woodpecker (*Dryobates borealis*)	Controlled	Ohio, United States	North America	Smoke generated by burning maple twigs, branches, and leaf litter.	No (only effects on habitat studied)	
Cahill & Walker 2000	Birds	Red-knobbed Hornbill (*Aceros cassidix*)	*In situ* (free-living)	Tangkoko-Dua Saudara Nature Reserve, Sulawesi, Indonesia	Asia	Smoke from 1997 wildfire.	Yes	Yes
Cheyne 2008	Mammals	Bornean white-bearded gibbon (*Hylobates albibarbis*)	*In situ* (free-living)	Natural Laboratory of Peat-swamp Forest, Indonesia	Asia	Smoke from 2006 wildfire. Months were categorized as "smoky" if the Indeks Standar Pencemar Udara (ISPU), an air quality index, exceeded Category 3 — indicative of unhealthy air quality (PM_{10} > 100 $\mu g/m^3$) — on more than 75% of days.	No	Yes
de Torrez et al. 2018	Mammals	Florida bonneted bat (*Eumops floridanus*)	*In situ* (free-living)	Fred C. Babcock-Cecil M. Webb Wildlife Management Area and Florida Panther	North America	Smoke from prescribed burns.	No	Yes

				National Wildlife Refuge, Florida, United States				
Dickinson et al. 2009	Mammals	Indiana bat (*Myotis sodalis*) and Northern long-eared bat (*Myotis septentrionalis*)	*In situ* (free-living)	Daniel Boone National Forest, Kentucky, United States	North America	Smoke from prescribed burns. CO peaked at ≥ 400 parts per million.	No	Yes
Dickinson et al. 2010	Mammals	Indiana bat (*Myotis sodalis*)	N/A (modeling exercise; data on air pollution from prescribed burns in Tar Hollow State Forest and Daniel Boone National Forest, United States)				No (no animals or specimens observed)	
Doty et al. 2018	Mammals	Gould's long-eared bat (*Nyctophilus gouldi*)	Controlled (captive)	Armidale, New South Wales, Australia	Australia	Smoke generated by burning eucalyptus leaves. Air quality measured using a smoke meter. Smoke level was measured at 6 (on a scale of 0 to 6), indicative of thick smoke.	No	Yes
Engstrom 2010	Multiple	Multiple	N/A (review, focused on first-order effects of fire in animals)				Yes	Yes
Erb et al. 2018	Mammals	Bornean orangutans (*Pongo pygmaeus wurmbii*)	*In situ* (free-living)	Tuanan Research Station, Central Kalimantan, Indonesia	Asia	Smoke from 2015 wildfire. During wildfire season, daily mean concentrations of PM$_{10}$ exceeded unhealthy levels (i.e., 150 μg/m$^{3)}$ most days (79%). PM$_{10}$ peaked at 1,829 μg/m^{3}.	Yes	Yes
Geiser et al. 2018	Mammals	Multiple (focus on small mammals)	N/A (review, focused on data from the southern hemisphere)				Yes	Yes
Hinz et al. 2018	Insects	Australian "firebeetle" (*Merimna atrata*)	Controlled (captive)	Insects collected in Perth, Western Australia. Experiment carried out in Bonn, Germany.	Europe	Insects exposed only to visual cues of smoke (e.g., projected image of a smoke plume).	No	Yes
Höcherl & Tautz 2015	Insects	European paper wasp (*Polistes dominula*)	Controlled (free-living)	Wüzberg, Germany	Europe	Smoke generated by burning poplar wood.	No	Yes
Hovick et al. 2017	Birds	Multiple (raptors)	*In situ* (free-living)	The Nature Conservancy Tallgrass Prairie Preserve and Oklahoma State University Cross Timbers Experimental Range in Oklahoma, United States.	North America	Smoke from prescribed burns.	No	Yes
Jordaan et al. 2020	Reptiles	Multiple (6 lizard and 8 snake species)	*In situ* (free-living)	Tembe Elephant Park, South Africa	Africa	Smoke from prescribed burns.	Yes	Yes

Klocke et al. 2011	Insects	*Microsania australis*, *Hypocerides nearcticus*, and *Anabarhynchus hyalipennis*	*In situ* (free-living)	Perth, Western Australia, Australia	Australia	Smoke from wildfires in 2006 to 2009.	No	Yes
Layne 2009	Mammals	Eastern red bat (*Lasiurus borealis*)	Controlled (captive)	Animals captured within and studied in outdoor enclosures at the Peck Ranch Conservation Area, Missouri, United States	North America	Smoke generated by burning leaf litter. CO peaked at 40 ppm.	No	Yes
Lee et al. 2017	Multiple (ecoacoustics study, soundscape likely dominated by birds and insects)		*In situ* (free-living)	"EcoLink" wildlife overpass connecting Bukit Timah Nature Reserve and Central Catchment Nature Reserve, Singapore	Asia	Smoke from 2015 wildfire. During smoke event, the Pollutant Standards Index (PSI) ranged from 97 to 267, indicative of moderate to very unhealthy air quality.	No	Yes
Liu et al. 2021	Insects	Painted lady butterfly (*Vanessa cardui* L.)	Controlled (captive)	London, England, United Kingdom	Europe	Smoke generated by burning incense. Concentrations of $PM_{2.5}$ during experiments ranged from 0.15 mg/m^3 to 1.28 mg/m^3.	No	Yes
Mendyk et al. 2020	Reptiles	Pinecone lizards (*Tiliqua rugosa*)	*In situ* (captive)	Audubon Zoo, New Orleans, Louisiana, United States	North America	Smoke not generated intentionally. Animals exposed to smoke when a pastry burned in a nearby toaster.	No	Yes
Milberg et al. 2015	Insects	Multiple	Controlled (free-living)	Ostergotland County, Sweden	Europe	Smoke generated by burning birch wood.	No	Yes
Nimmo et al. 2021	Multiple	Multiple	N/A (review, focused on behavioral responses to fire)				No	Yes
Nowack et al. 2016	Mammals	Eastern pygmy possum (*Cercartetus nanus*)	Controlled (captive)	Animals captured in Dorrigo, New South Wales, Australia. Study conducted in Armidale, New South Wales, Australia.	Australia	Possums exposed only to olfactory cues of smoke, specifically the scent of wood smoke.	No	Yes
Nowack et al. 2017	Mammals	Sugar gliders (*Petaurus breviceps*)	Controlled (captive)	Animals captured in the Dorrigo and Imbota Nature Reserves in New South Wales, Australia. Study	Australia	Smoke generated by burning branches, sawdust, and leaves. Air quality measured using a smoke meter. Smoke level was measured between 3.2 and 4.1	No	Yes

				conducted in Armidale, New South Wales, Australia.		(on a scale of 0 = clean air to 6 = thick smoke).		
O'Brien et al. 2006	Birds	Cuban parrot (*Amazona leucocephala*)	*In situ*	Great Abaco, Bahamas	North America	Smoke from a prescribed burn. The maximum CO_2 concentration in the surrogate nesting cavity was 2,092 ppm.	No (only effects on habitat)	
Sanderfoot & Gardner 2021	Birds	71 common bird species	*In situ* (free-living)	Washington, United States	North America	Smoke from wildfires in 2015 – 2018. Daily mean concentration of $PM_{2.5}$ ranged from 0 to 295.8 $\mu g/m^3$, with an average value of 8.6 $\mu g/m^3$.	No (only effects on detection studied)	
Sanderfoot & Holloway 2017	Birds	Multiple	N/A (review, focused on effects of air pollution on birds)				Yes	Yes
Scesny 2006	Mammals	Eastern red bat (*Lasiurus borealis*)	Controlled (captive)	Animals captured in the Peck Ranch Conservation Area in Missouri, United States. Study conducted in Springfield, Missouri, United States.	North America	Smoke generated by burning leaf litter.	No	Yes
Schütz et al. 1999	Insects	Black fire beetle (*Melanophila acuminata*)	Controlled (excised antennae)	Giessen, Germany	Europe	Excised antennae exposed to volatiles generated from burning pine.	No	Yes
Sensenig et al. 2017	Insects	*Crematogaster sjostedti*, *C. mimosae*, *C. nigriceps*, and *Tetraponera penzigi*	Controlled (free-living)	Mpala Research Centre, Kenya	Africa	Smoke generated by burning elephant dung.	No	Yes
Singer et al. 1989	Mammals	Elk (*Cervus elaphus*)	*In situ* (free-living)	Yellowstone National Park, United States	North America	Smoke from the 1988 wildfires.	Yes	Yes
Snoddy & Tippins 1968	Insects	*Microsania imperfecta*	*In situ* (free-living)	Clinch County, Georgia, United States	North America	Smoke from an incinerator.	No	Yes
Stawski et al. 2015	Mammals	Fat-tailed dunnart (*Sminthopsis crassicaudata*)	Controlled (captive)	Armidale, New South Wales, Australia	Australia	Smoke generated by burning eucalyptus.	No	Yes
Stawski et al. 2017	Mammals	Yellow-footed antechinus (*Antechinus flavipes*)	Controlled (captive)	Animals captured in the Aberbaldie Nature Reserve, New South Wales, Australia. Study conducted in Armidale, New South	Australia	Air quality measured using a smoke spot tester. Smoke level was measured at 5 (on a scale of 0 to 6), indicative of thick smoke.	No	Yes

				Wales, Australia, where animals were kept in outdoor enclosures.				
Tan et al. 2018	Insects	Squinty bush brown (*Bicyclus anynana*)	Controlled (captive)	National University of Singapore, Singapore	Asia	Smoke generated from burning incense. Average concentration of $PM_{2.5}$: 117 $\mu g/m^3$.	Yes	No
Thompson & Purcell 2016	Mammals	Fisher (*Pekania pennanti*)	*In situ*	Yosemite National Park and Sierra National Forest, United States	North America	Smoke from prescribed burns. The maximum CO concentration in dens ranged from 5.5 to 563.5 ppm, with a mean value of 170.8 ppm.	No (only effects on habitat studied)	
Tribe et al. 2017	Insects	Cape honeybee (*Apis mellifera capensis*)	*In situ* (free-living)	Table Mountain National Park, South Africa	Africa	Smoke from 2015 wildfire.	No	Yes
Venn-Watson et al. 2013	Mammals	Bottlenose dolphin (*Tursiops truncatus*)	*In situ* (free-living)	San Diego, California, United States	North America	Smoke from wildfires in 2003 and 2007. Maximum daily mean concentrations of $PM_{2.5}$ reported for study years: 170 mg/m^3 (2003) and 70 mg/m^3 (2007).	Yes	No
Visscher et al. 1995	Insects	Honey bee (*Apis mellifera*)	Controlled (excised antennae)	Riverside, California, United States	North America	Smoke generated by burning burlap.	No	Yes
Yang et al. 2021	Birds	Multiple species	*In situ* (free-living)	Western United States	North America	Smoke from 2020 wildfires.	Yes	No

2.8 DISCUSSION

We found that the available literature clearly demonstrates that wildfire smoke has direct and indirect effects on wildlife, including terrestrial and aquatic species (Figure 2.2, Table 2.1). Smoke inhalation contributes to adverse acute and chronic health outcomes in animals (Black et al., 2017; Venn-Watson et al., 2013), including CO poisoning, respiratory distress, neurological impairment, respiratory and cardiovascular disease, oxidative stress, and immunosuppression. These health effects could contribute to changes in wildlife activity, including movement (Erb et al., 2018) and vocalization (Cheyne, 2008). Animal behavior could also be influenced by changes in the physical environment that co-occur with smoke pollution, such as reduced sunlight or cooler air and water temperatures. Finally, many species that depend on fire-prone habitats have evolved to use smoke as a cue to engage in fire avoidance (Nimmo et al., 2021) or energy-conserving behaviors (Geiser et al., 2018) or perceive smoke as a signal of resource availability (Schütz et al., 1999). Both the immediate, direct effects of wildfire smoke on the health and behavior of animals and the long-term impacts of smoke on wildlife habitat could ultimately influence the demography of wildlife populations (Figure 2.2).

However, our review also demonstrates that a limited number of studies have investigated — or even considered — the impacts of wildfire smoke on wildlife (Table 2.1). For decades, naturalists have observed how wildlife respond to smoke from wildfires (e.g., Komarek, 1969; Braithwaite & Estbergs, 1987) and noted the vulnerability of animals exposed to smoke during wildfires or prescribed burns (e.g., Geluso et al., 1986). Yet, we found few peer-reviewed studies that directly investigated health outcomes or behavioral responses in wildlife associated with inhalation or detection of biomass smoke. After conducting a comprehensive search, we only identified 41 relevant studies, several of which did not explicitly test for an effect of smoke on animals and, instead, only considered how the presence of smoke could explain the responses observed (e.g., Cahill & Walker, 2000; Jordaan et al., 2020). Furthermore, research to date is unequally distributed across taxa (Figure 2.5) and world regions (Figure 2.4), with most studies conducted on mammals (39%) or insects (29%) in North America (37%), followed by Europe (17%) and Australia (15%) (Figure 2.4). Our keyword searches were conducted in English, which could have influenced the geographic distribution of the studies we reviewed.

Researchers have used a variety of methods to investigate the impacts of smoke on wildlife, which makes it challenging to compare findings across existing studies. Monitoring animals before, during, and after wildfires or prescribed burns (e.g., Dickinson et al., 2009; Jordaan et al., 2020) allows researchers to study how free-living animals respond to the onset and progression of a smoke event and enables direct inference about the impacts of biomass smoke on wildlife. However, such studies are difficult to plan, tend to be logistically complicated, and can jeopardize the health and safety of the research team (Erb et al., 2018). Alternatively, researchers have studied how animals respond to smoke generated in a controlled environment, such as a laboratory or outdoor enclosure (e.g., Nowack et al., 2018; Tan et al., 2018). This approach may be easier to implement because it does not require coordination with a fire management team or planning fieldwork around unpredictable wildfires. Controlled conditions also allow researchers to investigate specific health outcomes and behaviors in animals that would be difficult to assess in the wild. However, despite attempts to simulate biomass smoke that is representative of what animals would be exposed to during a wildfire smoke event in their natural habitat (e.g., Layne, 2009), controlled exposure experiments cannot reproduce the exact air quality and visibility conditions animals are likely to encounter in the wild. In addition, controlled studies are often limited to smaller species that are relatively easy to capture (e.g., insects, small mammals), and captive animals could exhibit behavioral changes during experiments that arise from confinement and should not be attributed to air pollution exposure (Sterner, 1993a, 1993b). In sum, the experience of smoke exposure for animals is likely to be vastly different between *in situ* and controlled studies, which makes it difficult to compare their findings.

Another limiting factor in connecting findings from existing research is the lack of robust air pollution measurements during field studies and experiments. Primary components of wildfire smoke include water vapor, CO_2, CO, PM, volatile organic compounds, nitrogen oxides, and hazardous air pollutants, such as acrolein, benzene, and formaldehyde (de Vos et al., 2009). However, the exact biological (Kobziar & Thompson, 2020) and chemical composition of smoke — and therefore its toxicity (Franzi et al., 2011; Kim et al., 2019) — is determined by fuel source (e.g., peat, oak, eucalyptus, etc.), combustion conditions (e.g., flaming, smoldering) (Hargrove et al., 2019; Kim et al. 2019), weather, topography, and long-range transport (Jalava et al., 2006). Without measuring the concentrations of reactive gases and aerosols animals are exposed to, it is impossible to construct dose-response relationships for specific health outcomes (Jaafar & Loh, 2014; Sanderfoot & Holloway, 2017). Furthermore, the composition of smoke could affect the visual and olfactory cues that elicit behavioral responses in wildlife. For example, Komarek (1969) observed that the behavior of Carolina grasshoppers (*Dissoteria carolina*) varied depending on smoke conditions — when exposed to dense, white smoke, the grasshoppers ceased all activity, yet when exposed to black smoke, grasshoppers exhibited fire avoidance behaviors. To facilitate comparisons and meta-analyses of findings across studies, it is critical that future investigations move beyond qualitative descriptions of smoke and actually quantify exposure by measuring concentrations of specific gases and aerosols (Engstrom, 2010; Sanderfoot & Holloway 2017).

More research is needed to identify which taxa and species are most threatened by wildfire smoke and determine how their vulnerability is influenced by physiology, behavior, and life-history strategy. It is well-established that birds are more sensitive to air pollution than other taxa (Brown et al., 1997) and therefore more likely to be susceptible than other animals to direct health effects associated with smoke inhalation. Cetaceans, like birds, exchange most of the air in their lungs with each breath, which might put them at greater risk than other mammals of experiencing adverse health outcomes during smoke events (Venn-Watson et al., 2013). Animal behavior and habitat use within and across species can also influence smoke exposure, thereby mediating risks. For example, bats that roost at higher heights are more protected from toxic gases during prescribed burns, and bats in torpor are less exposed to airborne toxins than they would be if they were active (Dickinson et al., 2009). Furthermore, overlap between the timing of smoke pollution episodes and life-history events likely contributes to species-specific vulnerability to wildfire smoke. For instance, birds attending to chicks (Cahill & Walker, 2000) or bats caring for pups (Dickinson et al., 2009) are likely more threatened by heat and smoke during fires than adults not tending to offspring, and fossorial reptiles are in greater danger when they come to the surface to feed or seek a mate (Jordaan et al., 2020). Comparing species distributions with spatial and temporal trends in air pollution could help wildlife managers determine if smoke should be considered alongside other threats, such as habitat degradation, when developing wildlife conservation plans.

Animals have evolved alongside wildfires for thousands of years, but megafires driven by climate change are generating novel disturbance stressors, such as large-scale smoke events, that could exert selective pressure on wildlife (Nimmo et al., 2021). The fire regimes species are adapted to are changing, and the traits that allow them to co-exist with fire and smoke may not be sufficient in the age of megafires (Nimmo et al., 2021). For example, typical fire avoidance behaviors might not be sufficient to protect wildlife from injury or morbidity during more severe, fast-moving fires (Engstrom, 2010; Nimmo et al., 2021), and even animals that are not in the direct path of fires can still be exposed to dangerous levels of wildfire smoke (Erb et al., 2018) (Figure 2.1). As climate change intensifies smoke pollution, more animals are at risk of acute and chronic health outcomes associated with smoke inhalation, which could lower survival and reproductive success (Figure 2.2). Over time, animals may adapt behavioral responses to detect hazardous air quality and limit their exposure to toxic gases and aerosols; however it is also possible that during large-scale smoke events, even well-adapted species may not find any refuge. Fire-adapted species might respond to visual and olfactory cues during large-scale smoke events even when fires are far away, which could have cascading impacts on wildlife communities. Pyrophilous species that rely on smoke as a cue to navigate toward burned areas may become disoriented during large-scale smoke events that occur hundreds of miles from fires, which could lead to reduced fitness and increased vulnerability to predation. Other species that use visual and olfactory cues from smoke to initiate fire-avoidance behaviors may do so at the expense of unnecessary energy expenditure when a fire is not an immediate threat (Dickinson et al., 2009). Animals that exhibit escape behaviors when it is smoky could also be more vulnerable to predation; natural history observations suggest that raptors hunt insects and small mammals at the edge of fires (Braithwaite & Estbergs, 1987) and may be attracted to smoke plumes as a signal of prey availability (Hovick et al., 2017). Additionally, prey species that have co-evolved with predators often use scent cues to detect predators (Blumstein et al., 2002); large-scale smoke events may affect the ability of prey to detect predators, further increasing their predation risk. Shifts in predator-prey interactions during smoke events could ultimately influence wildlife populations and community dynamics (Figure 2.2).

Earlier and more prolonged wildfire seasons might pose novel threats to species that now encounter wildfire smoke during a critical stage of their life cycle, such as reproduction or migration. For example, the breeding phenology of songbirds may increasingly overlap with the smoke season, which could adversely impact songbirds in a reproductive state. Individuals that breed earlier, thereby avoiding reproductive activities during peak smoke season, could have higher reproductive success. This could lead to the evolution of traits, such as more synchronous or asynchronous breeding (Iwasa & Levin, 1995), depending on the risks and benefits associated with the timing of breeding in relation to the threats posed by smoke events. Similarly, climate change is thought to be driving earlier breeding periods in many songbirds (Hällfors et al., 2020), a trend that could be reinforced as smoke pollution worsens air quality during the summer months. Although wildfire smoke could function as an ecological disturbance that forces some species to adapt their life-history strategies, it is unlikely that all species threatened by smoke pollution will be able to adapt their phenology to match changing environmental conditions (Both & Visser, 2001). More research is needed to assess how the frequency and timing of massive smoke events affects species adaptations to fire across different fire regimes.

We did not find any studies that explicitly linked wildfire smoke to demographic rates in wildlife populations (Figure 2.2); however, emerging evidence suggests that the impact of large-scale smoke events on survival of wildlife species could be substantial. Yang et al. (2021) found that air quality contributed to the spatial distribution of bird deaths in a mass avian mortality event in the Western U.S. in late summer 2020 (Yang et al., 2021). This was not the first study to suggest that air pollution has negative demographic consequences for bird populations — a recent study also found that reductions in ozone (O_3) pollution in the U.S. prevented the loss of more than one billion birds (Liang et al., 2020). Although O_3 is not a component of wildfire smoke, concentrations of O_3 can be higher on smoky days (Brey & Fischer, 2016). Smoke inhalation has also been implicated in the death of insects (Tan et al. 2018), reptiles (Jordaan et al., 2020), and mammals (Singer et al., 1989). Taken together, these findings emphasize the need to consider if and how wildfire smoke affects demographic rates in wildlife populations (Figure 2.2).

Shifts in animal behavior during wildfire smoke events might ultimately affect the probability of observing wildlife, which has important implications for wildlife research and monitoring. For example, animals that use smoke as cue to engage in fire-avoidance (e.g., burrowing) or energy-conserving behaviors (e.g., torpor) could be more difficult to observe during wildfire smoke events (Geiser et al., 2018). Sanderfoot & Gardner (2021) investigated how wildfire smoke affected detection of 71 common bird species in Washington, U.S. and found that particle pollution during the wildfire season influenced the probability of observing 37% of study species — as $PM_{2.5}$ increased, 16 species were less likely to be observed and 10 species were more likely to be observed. These results suggest that species-specific behavioral responses to wildfire smoke ultimately influence researchers' ability to detect wildlife. Failing to account for how smoke affects observations of wildlife could bias inference about wildlife activity and population demographics (Sanderfoot & Gardner, 2021).

Figure 2.6: Photo captures of wildlife in eastern Washington during the 2018 and 2020 wildfire seasons. A) Smoke settles in the valley behind a male white-tailed deer (*Odocoileus virginianus*). B) A group of mule deer (*Odocoileus hemionus*) navigate through thick smoke. C) Smoke obscures the view over a ridge as a coyote (*Canis latrans*) carries its prey. D) A wild turkey (*Meleagris gallopavo*) forages through haze. All photos were taken by camera traps deployed as part of the Washington Predator-Prey Project, a collaboration between the Washington Department of Fish & Wildlife and the University of Washington.

To develop effective policy for wildlife conservation, we must rapidly expand our understanding of the effects of wildfire smoke on wildlife. We believe that ecologists and wildlife managers are well-positioned to tackle this challenge by leveraging pre-existing resources and infrastructure to address critical knowledge gaps. For example, camera traps, GPS tags, and acoustic recorders are often deployed in fire-prone areas as part of long-term monitoring projects, many of which are likely to overlap with the wildfire season (Figure 2.6). Data collected by these instruments could be paired with long-term air quality monitoring data to investigate how wildfire smoke drives shifts in observations of wildlife (e.g., Lee et al., 2017) or explore specific behavioral responses to smoke pollution, such as movement and vocalization. This equipment could also be deployed to monitor wildlife before, during, and after prescribed burns. Studies of marked individuals pre- and post-fire could also provide insight into the direct effects of fires on demographic rates (Engstrom 2010). In addition, retrospective analyses of health records of captive animals housed in outdoor enclosures at zoos and aquariums could be used to assess how sudden, extreme smoke events influence the health of wildlife across a wide variety of taxa (Venn-Watson et al., 2013; Black et al., 2017). Finally, data from existing large-scale databases, such as the North American Breeding Bird Survey, eBird, eMammal, iNaturalist, Movebank, and Map of Life, could be used in correlative studies to link smoke exposure to observations of wildlife.

To facilitate comparison of future studies, we recommend that researchers at minimum a) identify the primary type of vegetation burned during prescribed burns or wildfires, or alternatively the substrate burned to generate smoke in controlled experiments and b) incorporate measurements of $PM_{2.5}$ during exposure. $PM_{2.5}$ is often the focus of epidemiological investigations into the impacts of wildfire smoke on public health (Aguilera et al., 2021; Liu et al., 2021; McClure & Jaffe, 2018); as such, there is a multitude of resources available to characterize particle pollution during smoke events or controlled experiments, including data from ground-based air pollution sensors, air quality models, and satellite instruments (Diao et al., 2019). Data from ground-based air quality monitors are considered the “gold standard” for estimating exposure to air pollution (Diao et al., 2019) and are often available to the public —

for example, the U.S. Environmental Protection Agency provides data on air pollution across the United States, Puerto Rico, and the U.S. Virgin Islands on the web at https://www.epa.gov/outdoor-air-quality-data. If data from ground-based monitors is not available at relevant spatial and temporal scales, atmospheric scientists might rely on statistical interpolation or Land-Use Regression (LUR) models to build $PM_{2.5}$ exposure estimates (Jerrett et al., 2005; Zou et al., 2009). Alternatively, output from chemical transport models (CTMs) can be used in retrospective analyses and forecasting (Zou et al., 2009). CTMs simulate air pollution by modeling transformation and transport of emissions (Jerrett et al., 2005); examples of CTMs include the Community Model for Air Quality (CMAQ) and the Weather Research and Forecasting Model – Chemistry (WRF-Chem). Satellite data are also increasingly used to build $PM_{2.5}$ exposure estimates, although measurements from instruments on polar-orbiting satellites are only available once or twice a day (Diao et al., 2019; West et al., 2016). Some of these approaches could be readily implemented with minimal training (Diao et al., 2019), but others require technical knowledge. Regardless, careful consideration of the location and behavior of the target population is essential in determining exposure to specific pollutants. We recommend that ecologists studying the impacts of wildfire smoke on wildlife collaborate with atmospheric scientists to build $PM_{2.5}$ exposure estimates using the best available tools.

2.9 CONCLUSION

The frequency and severity of large-scale smoke events are increasing as climate change intensifies global wildfire activity (Abatzloglou & Williams, 2016; Westerling et al., 2011), posing new risks to wildlife (Nimmo et al., 2021). Despite substantial research linking wildfire smoke to adverse health outcomes in humans, few studies have investigated the physiological and behavioral responses to wildfire smoke in animals (Figure 2.4, Table 2.1) (Erb et al. 2018;

Geiser et al. 2018). However, research to date suggests that smoke inhalation contributes to negative acute and chronic health outcomes in a diversity of air-breathing animals, including mammals, birds, reptiles, and insects (Figure 2.2, Table 2.1). Detection of smoke triggers fire-avoidance and/or energy-conserving behaviors in some wildlife species, and some species use smoke as a cue to navigate toward fires to take advantage of resources available in burned habitats (Figure 2.2). However, even species that are adapted to fire-prone habitats are at risk of health outcomes linked to smoke inhalation, and it is unclear how they will cope with more extreme smoke pollution episodes. To inform the study and conservation of wildlife in a rapidly warming world, it is imperative that we expand our knowledge of wildfire smoke impacts on wildlife. Bridging the divide between the disciplines of ecology and atmospheric science will be essential in meeting this goal. We strongly recommend that scientists and managers build interdisciplinary partnerships and leverage existing data sets, infrastructure, and tools to quickly and efficiently address knowledge gaps and tackle research questions of global importance.

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Chapter 3. WILDFIRE SMOKE AFFECTS DETECTION OF BIRDS IN WASHINGTON STATE

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Abstract: Wildfire smoke is likely to have direct health effects on birds, as well as influence movement, vocalization, and other avian behaviors. These behavioral changes may affect if and how birds are observed in the wild, although research on the effects of wildfire smoke on bird behavior is limited. To evaluate how wildfire smoke affects detection of birds, we combined data from eBird, an online community science program, with data from an extensive network of air quality monitors in the state of Washington over a 4-year period. We assessed how $PM_{2.5}$, a marker of smoke pollution, affected the probability of observing 71 bird species during the wildfire seasons of 2015 – 2018 using bird observations from 62,908 eBird checklists. After accounting for habitat, weather conditions, seasonality, and survey effort, we found that $PM_{2.5}$ affected the probability of observing 37% of study species. The ambient concentration of $PM_{2.5}$ was negatively associated with the probability of observing 16 species and positively associated with the probability of observing 10 species, indicating that birds exhibit species-specific behavioral changes during wildfire smoke events that influence how they are observed. Our results suggest that wildfire smoke impacts the presence, availability, and/or perceptibility of birds. Impacts of smoke pollution on human observers, such as impaired visibility, may also influence detection of birds. These results provide a foundation for developing mechanistic hypotheses to explain how birds, and our studies of them, are impacted by wildfire smoke. Given the projected increase in large-scale wildfire smoke events under future climate change scenarios, understanding how birds are affected by wildfire smoke — and how air pollution may influence our ability to detect them — are important next steps to inform wildlife research and avian conservation. *Keywords:* air pollution, fine particulate matter, presence, detection, eBird

3.1 INTRODUCTION

Large-scale wildland fires pose direct threats to wildlife, including mortality, injury, and health effects from exposure to high ambient temperatures and the toxic gases and aerosols found in smoke (Engstrom, 2010), such as fine particulate matter ($PM_{2.5}$, i.e., suspended solid or liquid particles with an aerodynamic diameter < 2.5 μm) (O'Dell et al., 2019). Although exposure to $PM_{2.5}$ from wildfire smoke has known, adverse impacts on human health (Cascio, 2018; Wettstein et al., 2018), few studies have been conducted on how wildfire smoke affects the health and behavior of free-living, non-human animals (Cheyne, 2008; Lee et al., 2017; Sanderfoot & Holloway, 2017; Erb et al., 2018). Such responses may affect if and how wildlife are observed, yet the impacts of wildfire smoke on detection of wildlife species have not previously been explored.

Birds may exhibit behavioral changes during wildfire smoke events. Lee et al. (2017) showed that acoustic indices used to characterize bird activity declined for months at a location after it was inundated with smoke from wildfires, suggesting that birds altered their singing behavior, vacated the area, or died. Behavioral changes exhibited by birds and other animals in response to wildfire smoke may signal immediate, underlying health effects (Black et al., 2017). However, other changes in the physical environment during smoke pollution episodes, such as cooler air temperatures (Robock, 1991) and reduced visibility (Haider et al., 2019), could also trigger behavioral responses in wildlife (Cheyne, 2008).

Changes in avian behavior during wildfire smoke events could affect the probability of observing birds. For example, if wildfire smoke prompts a species to relocate, we would expect the probability of observing that species to be inversely related to the outdoor concentration of $PM_{2.5}$, a marker of smoke pollution. However, the probability of observing a species reflects both whether or not a species is present and if so whether or not it is observed (i.e., detected). Even if the presence of birds is unaffected by wildfire smoke, birds may change their behavior during smoke events in such a way that they are more or less likely to be observed. For example, if birds sing less or reduce their overall activity as smoke pollution from wildfires increases, they would be more difficult to observe due to a decline in the visual and auditory cues used to detect them. Alternatively, if wildfire smoke prompts birds to fly faster or congregate in larger groups, they would likely be easier to detect. Changes in the probability of observing a species during wildfire smoke events may therefore reflect behavioral responses to wildfire smoke that drive variation in presence, availability, and perceptibility, as well as any direct mortality.

Impacts of smoke pollution on human observers may also influence the probability of observing birds during wildfire smoke events. Detection of avifauna may be negatively impacted if wildfire smoke impairs the observational skills of birders, either due to acute health impacts or reduced visibility; this would lead to a decrease in the probability of observing avian species that is independent of bird behavior.

To explore how the probability of observing birds changes during wildfire smoke events, we combined data from eBird, a semi-structured community science program run by the Cornell Lab of Ornithology, with long-term monitoring data of outdoor concentrations of $PM_{2.5}$. eBird is a global community science program that collects bird observations submitted by volunteers in a checklist format (Sullivan et al., 2009). Due to the program's popularity, the eBird database contains more than 600 million records, submitted by hundreds of thousands of participants from around the world. Community science programs like eBird facilitate the collection of ecological data at greater spatial and temporal scales than what is possible within a traditional science framework. However, eBird data are collected opportunistically by volunteers who differ in experience, training, skill, and objectivity, leading to spatial, temporal, taxonomic, and observer biases (Johnston et al., 2019). In our analysis, we used several variables to account for heterogeneity in sampling events and among observers, including time and duration of surveys and distance traveled by observers.

In this study, we estimated the effect of $PM_{2.5}$ on the probability of observing 71 bird species during the wildfire season in Washington, USA. Due to the potential effects of smoke pollution on avian behavior and perceptibility, we hypothesized that the concentration of $PM_{2.5}$ would be an important predictor of the probability of observing birds. More specifically, we expected that species with larger home ranges may be better able to emigrate from an area impacted by wildfire smoke pollution than birds with smaller home ranges, and therefore that the probability of observing them would be inversely related to the concentration of $PM_{2.5}$. We also expected that the probability of observing avian species primarily detected by ear would decrease as smoke pollution increased, due to previous research linking declines in bird vocalization to wildfire smoke exposure (Lee et al., 2017). Finally, we expected that detection of birds often observed at far distances, such as diurnal raptors and gulls, would decrease during smoke events due to reductions in visibility. Our study provides a foundation for developing mechanistic hypotheses to explain interspecific behavioral responses to wildfire smoke and highlights the need to consider how air pollution affects our observations of birds and other wildlife. Given the projected increase in large-scale wildfire smoke events under future climate change scenarios (Westerling et al., 2006; Jacob & Winner, 2009), these efforts are critical to inform ornithological research, wildlife management, and avian conservation.

3.2 METHODS

3.2.1 *Study Area*

Washington, USA, is a large state with many habitat types, including wet and dry forests, shrubland, marshes, and urban and suburban areas (Washington Department of Fish and Wildlife, 2015). Hundreds of wildfires occur in the state each year, burning tens thousands of acres — more than 400,000 acres were burned by wildfires in 2018 alone (Washington State Academy of Sciences, 2019). Smoke events driven by large-scale wildfires in 2015, 2017, and 2018 subjected both people and wildlife in Washington state to hazardous air quality, as indicated by high concentrations of $PM_{2.5}$ (Figure 3.1). Levels of $PM_{2.5}$ during these smoke pollution episodes were at times much higher than the National Ambient Air Quality Standard (NAAQS) of 35 $\mu g/m^3$ (United States Environmental Protection Agency, 2016; Figure 3.1). Due to extensive wildfires, air pollution during the 2018 wildfire season was higher in some parts of Washington state than anywhere else in the world (Washington State Academy of Sciences, 2019).

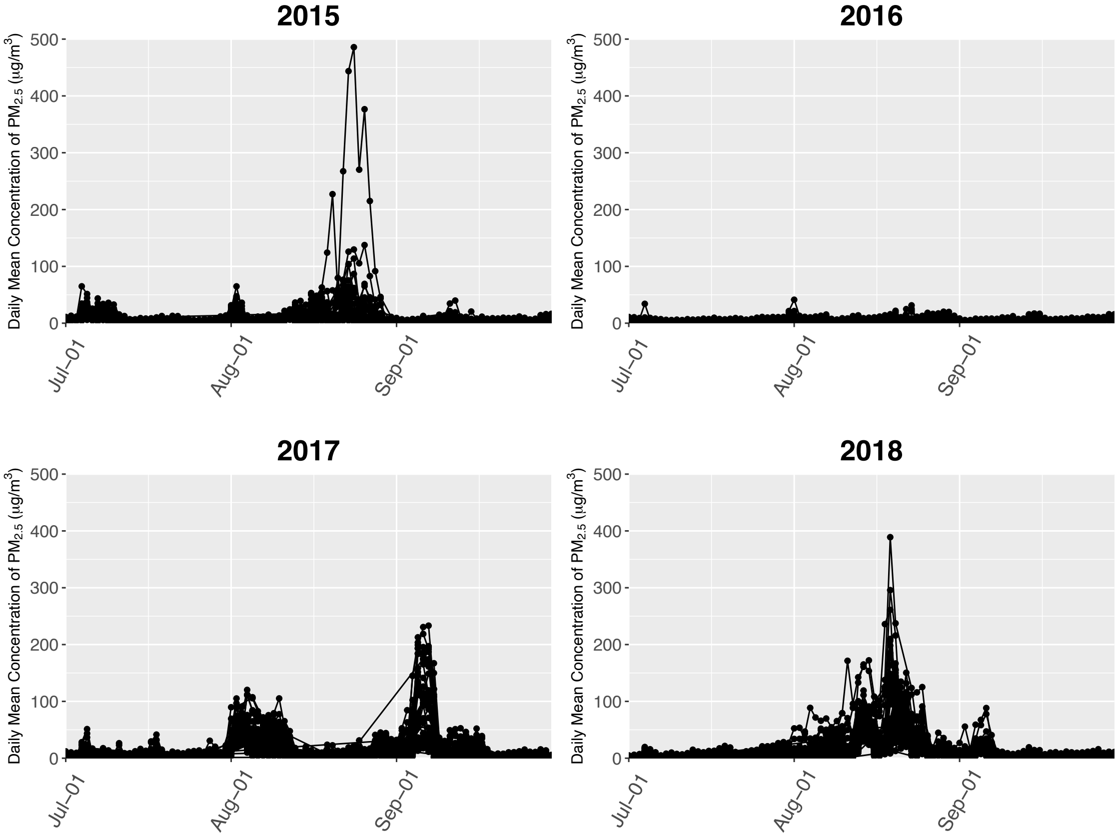

Figure 3.1: Wildfire smoke events are marked by abrupt peaks in $PM_{2.5}$, suspended solid and liquid particles smaller than 2.5 microns in diameter that pose health risks to both people and wildlife. These plots show the daily mean concentration of $PM_{2.5}$ at air quality monitors in the state of Washington during the wildfire season (July, August, and September) in 2015 through 2018. Each point represents a measurement from one air quality monitor. Large-scale smoke events occurred in 2015, 2017, and 2018; note the sudden increases in ambient $PM_{2.5}$. The y-axis ranges from 0 to 500 $\mu g/m^3$. The National Ambient Air Quality Standard for $PM_{2.5}$ is only 35 $\mu g/m^3$. These plots illustrate that exposure to particle pollution during the wildfire season often exceeds levels deemed safe for public health.

3.2.2 *Data Collection*

3.2.2.1 Bird Observations

We analyzed bird observations collected by the public and submitted to eBird (eBird Basic Dataset, 2021). eBird supports opportunistic data collection by volunteers who submit online checklists of species they observe and other related information (e.g., date, time, duration and type of survey, distance traveled, number of observers, etc.) (Sullivan et al., 2009). We extracted all bird observations documented in Washington state from July 1 – September 30, 2015 – 2018 from the eBird Basic Dataset (eBird Basic Dataset, 2021). We used the *auk* package (Strimas-Mackey et al., 2018) in R (R Core Team, 2020) to filter bird observations to include only those from stationary, traveling, and area counts. Stationary surveys take place within 30 meters of a point location, traveling surveys are conducted along a route of known distance, and area surveys are carried out in an area of known size. We chose to include all three types of surveys in our analysis because wildfire smoke events are of short duration and we wanted to ensure that we included bird observations on days when air quality was poor. Stationary checklists were assigned a distance traveled of 0 meters. To estimate a distance traveled for area checklists, we assumed the area surveyed was a square and the distance traveled was two times the length of one side of the square. We also restricted our dataset to only include bird observations from complete checklists — those for which observers indicated that they recorded all of the species that they detected during a survey. By excluding incomplete checklists, we were able to infer when species were not detected, as opposed to simply not recorded by an observer, thereby strengthening our inference (Johnston et al., 2019).

Next, we used the *geosphere* package (Hijmans, 2019) in R (R Core Team, 2020) to spatially filter the data to include only bird observations from checklists with locations within 32 kilometers of an active $PM_{2.5}$ monitor in Washington state. Data from ground-based air quality sensors are often used to inform public health; however, measurements from air quality sensors are only representative of exposure to air pollution in close proximity. We therefore restricted our data set to observations near air quality monitoring sites to ensure that the measurements of $PM_{2.5}$

at those locations would serve as reasonable estimates of exposure to this pollutant where birds were observed. We specifically chose a distance of 32 kilometers to align with the spatial resolution of the weather data used in our analysis. This distance is also within the range of threshold distances used when characterizing exposure to air pollution in public health research. If the distance an eBirder traveled exceeded 32 kilometers, they may have been birding outside a 32-kilometer radius from the nearest air quality monitor; to negate this possibility, we excluded any checklists with a distance traveled greater than 32 kilometers.

We focused on commonly observed species in our analysis because we wanted to compare responses to wildfire smoke across a large set of species, but we needed to ensure that there were a sufficient number of detections of those species to fit our models. We used the filtered data to select our study species. We included all species with at least 750 detections in 2015, the baseline year. Seventy-one species met this criterion (see Table 3.1 for a complete list of study species). We used the *auk* package to generate detection/non-detection data for each study species (Strimas-Mackey et al., 2018). We then linked each of the checklists to the daily concentration of $PM_{2.5}$ at the monitoring station closest to the checklist location. We eliminated checklists for which we could not assign a daily concentration of $PM_{2.5}$ from the nearest ground-based air quality monitor. Data on $PM_{2.5}$ were not available from every monitor on every date of our study period because not all monitors measure particle pollution continuously.

Table 3.1: List of the 71 study species included in this analysis. Species are listed by common name, in order of how often they were detected in the checklists included in our final dataset. Complete model results for all study species are reported in Appendix C.

Common name	Scientific name
American Robin	*Turdus migratorius*
Black-capped Chickadee	*Poecile atricapillus*
American Crow	*Corvus brachyrhynchos*
Song Sparrow	*Melospiza melodia*
Northern Flicker	*Colaptes auratus*
Great Blue Heron	*Ardea herodias*
Barn Swallow	*Hirundo rustica*
Mallard	*Anas platyrhynchos*
American Goldfinch	*Spinus tristis*
Spotted Towhee	*Pipilo maculatus*
European Starling	*Sturnus vulgaris*
House Finch	*Haemorhous mexicanus*
Cedar Waxwing	*Bombycilla cedrorum*
Steller's Jay	*Cyanocitta stelleri*
Anna's Hummingbird	*Calypte anna*
Canada Goose	*Branta canadensis*
Dark-eyed Junco	*Junco hyemalis*
White-crowned Sparrow	*Zonotrichia leucophrys*
Glaucous-winged Gull	*Larus glaucescens*
Belted Kingfisher	*Megaceryle alcyon*
Red-breasted Nuthatch	*Sitta canadensis*
Bewick's Wren	*Thryomanes bewickii*
Killdeer	*Charadrius vociferus*
Chestnut-backed Chickadee	*Poecile rufescens*
California Gull	*Larus californicus*
Osprey	*Pandion haliaetus*
Rock Pigeon	*Columba livia*
Red-winged Blackbird	*Agelaius phoeniceus*
Double-crested Cormorant	*Phalacrocorax auritus*
Caspian Tern	*Hydroprogne caspia*
Eurasian Collared-Dove	*Streptopelia decaocto*
Violet-green Swallow	*Tachycineta thalassina*
Common Raven	*Corvus corax*
House Sparrow	*Passer domesticus*
Savannah Sparrow	*Passerculus sandwichensis*
Bald Eagle	*Haliaeetus leucocephalus*
Common Yellowthroat	*Geothlypis trichas*
Mourning Dove	*Zenaida macroura*
Red-tailed Hawk	*Buteo jamaicensis*

Downy Woodpecker	*Dryobates pubescens*
Ring-billed Gull	*Larus delawarensis*
Swainson’s Thrush	*Catharus ustulatus*
Pied-billed Grebe	*Podilymbus podiceps*
Least Sandpiper	*Calidris minutilla*
Bushtit	*Psaltriparus minimus*
Brown Creeper	*Certhia americana*
Western Sandpiper	*Calidris mauri*
Pigeon Guillemot	*Cepphus columba*
Golden-crowned Kinglet	*Regulus satrapa*
Yellow-rumped Warbler	*Setophaga coronata*
Western Wood-Pewee	*Contopus sordidulus*
Heermann’s Gull	*Larus heermanni*
Turkey Vulture	*Cathartes aura*
Black-headed Grosbeak	*Pheucticus melanocephalus*
Yellow Warbler	*Setophaga petechia*
Brown-headed Cowbird	*Molothrus ater*
Orange-crowned Warbler	*Leiothlypis celata*
Western Tanager	*Piranga ludoviciana*
Wood Duck	*Aix sponsa*
Marsh Wren	*Cistothorus palustris*
Greater Yellowlegs	*Tringa melanoleuca*
Tree Swallow	*Tachycineta bicolor*
Gadwall	*Mareca strepera*
Pelagic Cormorant	*Phalacrocorax pelagicus*
California Quail	*Callipepla californica*
Green-winged Teal	*Anas crecca*
Brewer’s Blackbird	*Euphagus cyanocephalus*
Spotted Sandpiper	*Actitis macularius*
Rhinoceros Auklet	*Cerorhinca monocerata*
American Coot	*Fulica americana*
Northern Harrier	*Circus hudsonius*

3.2.2.2 Environmental Data

To characterize the ambient concentration of $PM_{2.5}$ at checklist locations, we used data from the Environmental Protection Agency (EPA) Air Quality System (AQS) (United States Environmental Protection Agency, 2019). We downloaded daily $PM_{2.5}$ concentrations (24-hour averages) available from all ground-based $PM_{2.5}$ monitors in the state of Washington for the years 2015 through 2018. (For more information on how we processed air quality data, see Appendix B.) Only one checklist was linked to a $PM_{2.5}$ concentration greater than 300 μg/m^3. The $PM_{2.5}$ measurements at this location the day before and after the observation date of this checklist were much lower; we therefore removed this value as an outlier. In our final dataset, the daily concentration of $PM_{2.5}$ ranged from 0 μg/m^3 to 295.8 μg/m^3, with a mean value of 8.6 μg/m^3.

To account for how weather may influence the probability of observing birds, we used data from the North American Regional Reanalysis (NARR) to determine daily mean air temperature and daily accumulated precipitation for each eBird checklist. NARR data were provided by the National Oceanic and Atmospheric Administration Physical Sciences Laboratory in Boulder, Colorado, USA from their website at https://psl.noaa.gov/. The spatial resolution of NARR data is approximately 32 kilometers. We used the *ncdf4* package (Pierce, 2019) in R (R Core Team, 2020) to extract the weather data.

We also incorporated land cover as a predictor because we expected that the 71 study species would have different habitat requirements and preferences. We assigned a land cover type to each checklist using data from the 2016 National Land Cover Database (NLCD), developed by the Multi-Resolution Land Characteristics (MRLC) Consortium and made available as a layer in ArcMap by the Environmental Systems Research Institute (Esri) (Esri, 2019, 2020). Land cover classifications were grouped into nine categories: open water, perennial ice/snow, developed, barren, forest, shrubland, herbaceous, planted/cultivated, and wetlands. Prior to analysis, we removed checklists for which a land cover type could not be determined because the checklist locations fell outside the bounds of the NLCD. We also eliminated checklists that were assigned a land cover class of “perennial ice/snow” because very few checklists fell into this category.

Our final dataset included detection/non-detection data for 71 species from 62,908 eBird checklists, each of which represented a single survey. These checklists were submitted by 4,865 unique eBird observers and linked to air quality data from a total of 71 $PM_{2.5}$ sensors. A map showing the locations of eBird checklists and air quality monitoring sites included in our analysis is shown in Figure 3.2. This map was created using the *rnaturalearth* (South, 2017) and *sf* (Pebesma, 2018) packages in R (R Core Team, 2020).

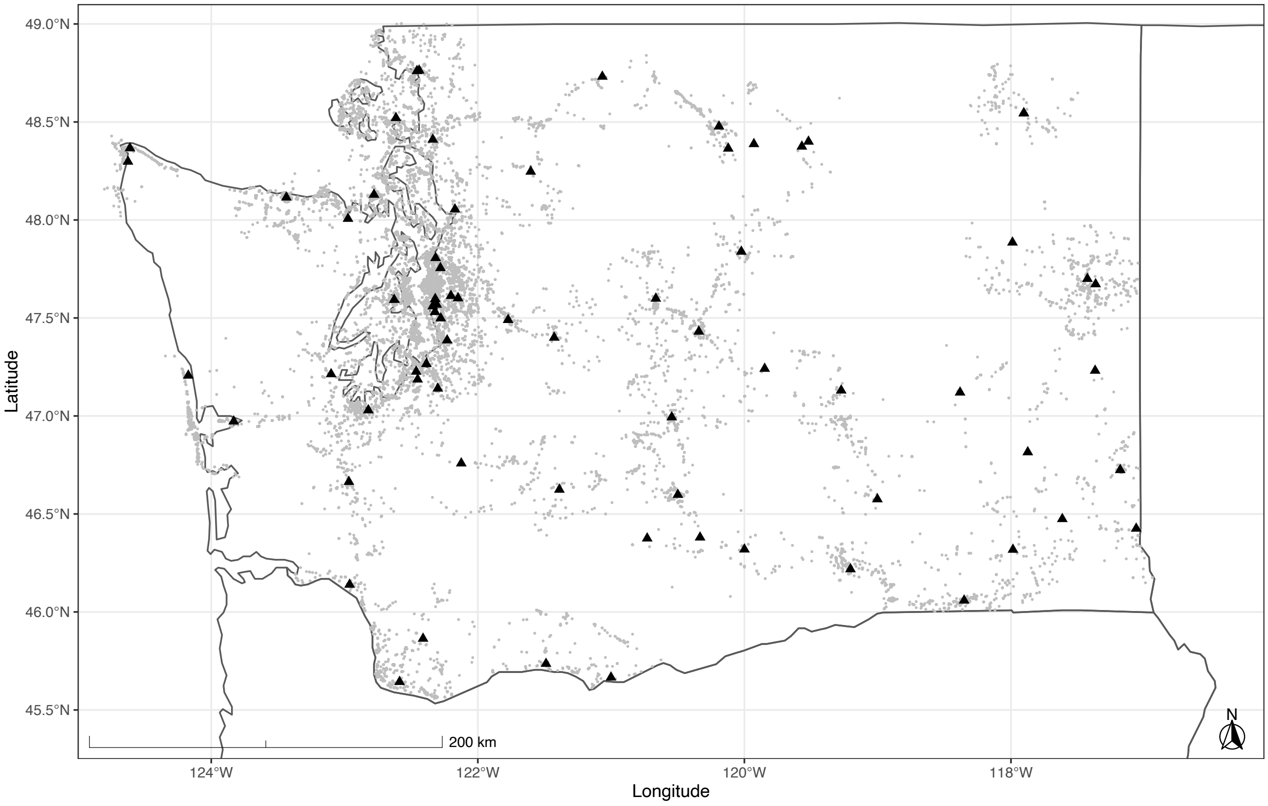

Figure 3.2: Map of Washington showing the locations of 62,908 eBird checklists included in our analysis as gray dots. The locations of the 71 air quality monitoring sites included in our analysis are marked as black triangles.

3.2.3 *Statistical Analysis*

We used generalized linear mixed models with a binomial distribution to model the probability of observing each of the 71 study species during the 2015 – 2018 wildfire seasons. Each model included fixed effects of 8 numeric variables (day of year, day of year squared, time observations started, duration of survey, distance traveled, daily mean air temperature, daily accumulated precipitation, and daily concentration of $PM_{2.5}$), 2 categorical variables (year and land cover class), and a random effect of individual observer. For each of the 71 study species, we modeled p_i, the probability that a species is observed in checklist i, as:

$$logit(p_i) = \alpha_0 + \alpha_1 * year_i + \alpha_2 * land\ cover\ class_i + \alpha_3 * day_i + \alpha_4 * day_i^2 + \alpha_5 * time_i + \alpha_6 * duration_i + \alpha_7 * distance_i + \alpha_8 * temp_i + \alpha_9 * precip_i + \alpha_{10} * PM_{2.5_i}$$

We allowed the intercept α_0 to vary by unique observer as a random effect to account for differences in skill, knowledge, and experience among eBird observers as well as a lack of independence in their checklists. In addition to the environmental variables (land cover, temperature, precipitation, and $PM_{2.5}$), we included day of year and day of year squared to account for seasonal variation in species presence, which may take a linear or quadratic shape. We included time of day because it is well known that birds exhibit daily activity patterns, which directly influences detection of many species (Robbins, 1981a; Johnson, 2008). We also included the duration of a survey in minutes because we expected that the more time eBirders spent birding, the more likely they would be to observe birds. We included distance traveled to capture additional variation in surveys. To account for annual variation in population demographics, we included a year effect term. All numeric variables were standardized. Prior to analysis, we compared all continuous variables for potential collinearity (see Appendix D for the full correlation matrix).

Each model was fit using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2020). We calculated conditional R^2 values to assess model fit (Lüdecke et al., 2019). We used an information theoretic approach (Akaike's Information Criterion (AIC)) to first evaluate the overall important of $PM_{2.5}$ by comparing the full model to the same model without $PM_{2.5}$. We anticipated that AIC might select the model with $PM_{2.5}$ even when the effect was not statistically significant due in part to the large size of the dataset. We therefore used p-values and 95% confidence intervals on the effect of $PM_{2.5}$ in the full model to determine if this predictor was statistically significant ($p < 0.05$) for any of the 71 study species.

We were concerned that the number of checklists submitted may decline during smoke events. To test this, we used a generalized linear mixed model (GLMM) to assess how the number of checklists varied with the level of risk posed by particle pollution. We binned $PM_{2.5}$ into 3 categories based on current public health standards: good to moderate (< 35.5 µg/m^3), unhealthy for sensitive groups ($>= 35.5$ and < 55.5 µg/m^3), and unhealthy to hazardous ($>= 55.5$ µg/m^3). We then ran a negative binomial GLMM with the total number of checklists as the response variable, $PM_{2.5}$ as a fixed effect, and air quality monitor as a random effect. We included air quality monitor as a random effect because some monitors are located in more densely populated areas.

3.3 RESULTS

Based on our model selection using AIC, the top model included the effect of ambient concentration of $PM_{2.5}$ for 37 of the 71 study species (52%). Of those 37 species, $PM_{2.5}$ had a statistically significant effect on the probability of observing 26 of the 71 study species (36.6%) (Figure 3.3). The probability of observing birds decreased with elevated concentrations of $PM_{2.5}$

for 16 of these 26 species, including Great Blue Heron (*Ardea herodias*), Canada Goose (*Branta canadensis*), Killdeer (*Charadrius vociferus*), California Gull (*Larus californicus*), Osprey (*Pandion haliaetus*), Double-crested Cormorant (*Phalacrocorax auritus*), Caspian Tern (*Hydroprogne caspia*), Savannah Sparrow (*Passerculus sandwichensis*), Bald Eagle (*Haliaeetus leucocephalus*), Red-tailed Hawk (*Buteo jamaicensis*), Bushtit (*Psaltriparus minimus*), Heermann's Gull (*Larus heermanni*), Turkey Vulture (*Cathartes aura*), Marsh Wren (*Cistothorus palustris*), Greater Yellowlegs (*Tringa melanoleuca*), and Northern Harrier (*Circus hudsonius*) (Figure 3.3). The concentration of $PM_{2.5}$ was positively related to the probability of observing 10 species: Spotted Towhee (*Pipilo maculatus*), Cedar Waxwing (*Bombycilla cedrorum*), Red-breasted Nuthatch (*Sitta canadensis*), Yellow-rumped Warbler (*Setophaga coronata*), Black-headed Grosbeak (*Pheucticus melanocephalus*), Yellow Warbler (*Setophaga petechia*), Brown-headed Cowbird (*Molothrus ater*), Orange-crowned Warbler (*Leiothlypis celata*), Western Tanager (*Piranga ludoviciana*), and California Quail (*Callipepla californica*) (Figure 3.3). No consistent pattern was observed in the direction of other temporal and environmental predictors included in our models for these 26 species. We did not find evidence that air quality influenced the total number of eBird checklists submitted, which suggests that the frequency of checklist submissions by eBirders was not affected by outdoor concentrations of $PM_{2.5}$ during our study period in Washington state.

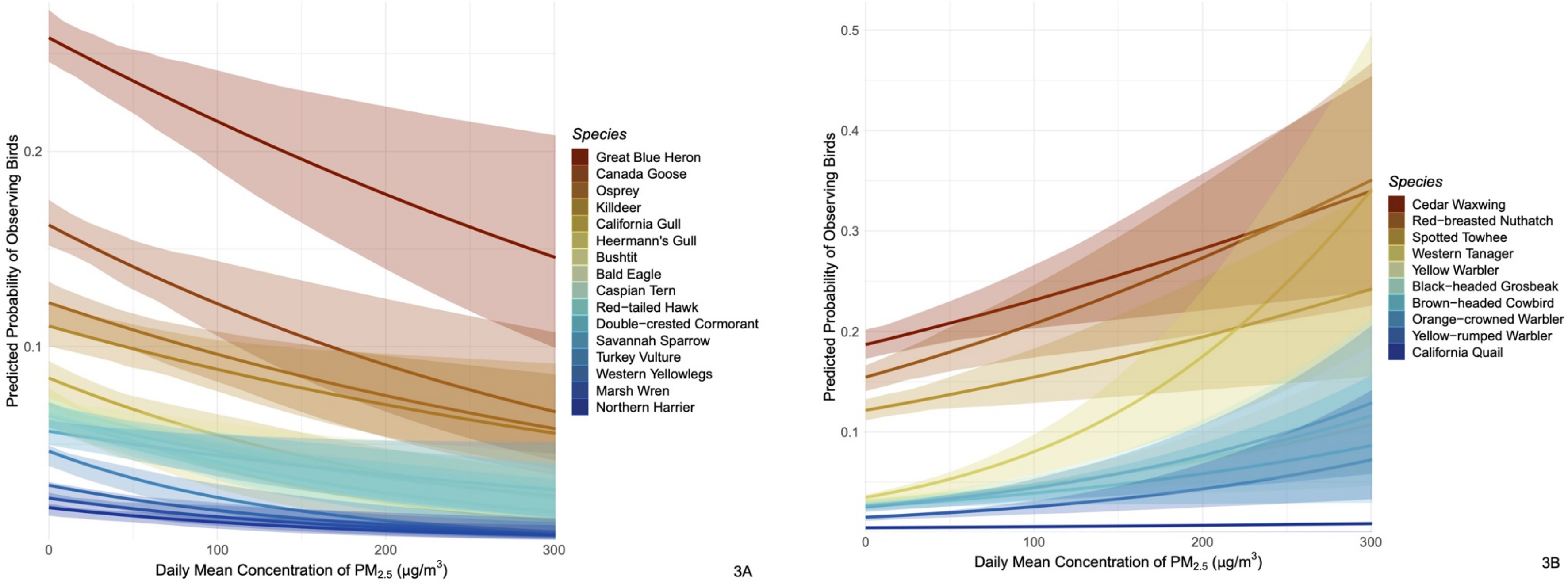

Figure 3.3: PM$_{2.5}$ influenced the detection of 26 of the 71 study species included in our analysis. Here we show the predicted probability of observing a species at daily concentrations of PM$_{2.5}$ ranging from 0 to 300 μg/m^3 in the year 2015 in developed areas, assuming average levels of all other predictors. Species with a negative association are shown in (A) and those with a positive association are shown (B). Each color represents predictions for one species. Solid lines indicate median predictions and ribbons illustrate bootstrapped 95% confidence intervals. Color palette provided by Pedersen & Crameri (2021).

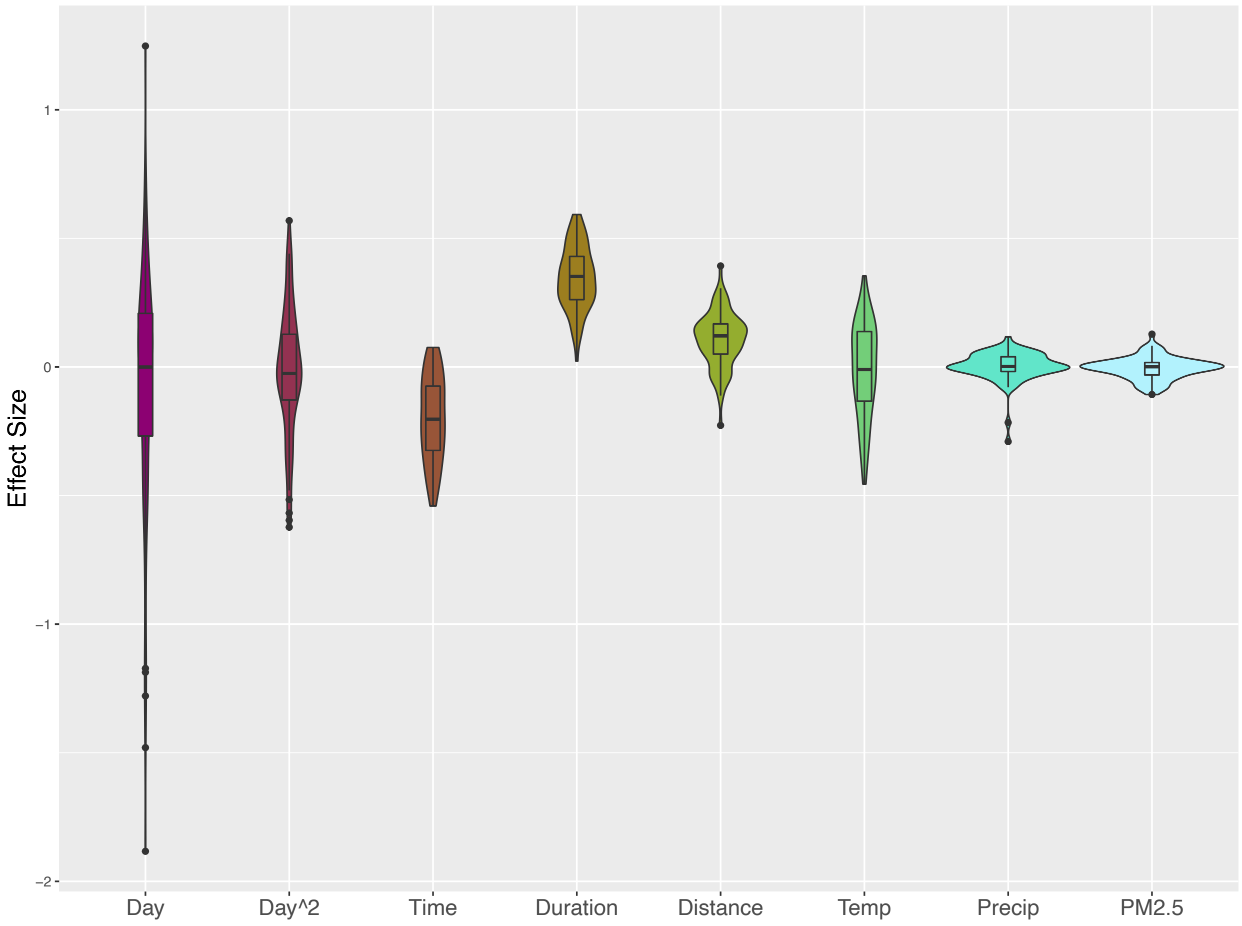

Figure 3.4: Although small, the effect of $PM_{2.5}$ on the probability of observing birds sometimes exceeded the effect of weather and other temporal and environmental predictors known to influence detection of birds. These violin plots show the probability density of the effect sizes (coefficient estimates on the logit scale) for the eight numeric temporal and environmental predictors included in the logistic regression analysis for all 71 study species. The box plots within each violin plot denote the median and interquartile range. Predictors include day of year (Day), day of year squared (Day^2), time observations started (Time), duration of survey (Duration), distance of survey (Distance), daily mean air temperature (Temp), daily accumulated precipitation (Precip), and daily concentration of fine particulate matter (PM2.5). Color palette provided by Pedersen and Crameri (2021).

The effect of year, land cover class, day of year, day of year squared, time observations started, daily mean air temperature, daily accumulated precipitation, duration of survey, and distance traveled varied by species (Figure 3.4). As expected, duration of survey was consistently a positive predictor of the probability of observing birds — the longer eBirders were in the field, the more likely they were to observe each species in the study (Figure 3.4). This effect was statistically significant ($p < 0.05$) for all species included in our analysis except for Brewer's Blackbird (*Euphagus cyanocephalus*). Detection of most species was positively related to distance traveled; however, distance was a statistically significant, negative predictor ($p < 0.05$) of the probability of observing 9 of the 71 study species. These species included common backyard birds (i.e., American Goldfinch (*Spinus tristis*), House Finch (*Haemorhous mexicanus*), Anna's Hummingbird (*Calypte anna*)), as well as shorebirds (i.e., Western Sandpiper (*Calidris mauri*), Least Sandpiper (*Calidris minutilla*), Greater Yellowlegs). In addition, the time observations started was a statistically significant, negative predictor ($p < 0.05$) of the probability of observing 58 of the 71 study species, indicating that the probability of observing most species decreased throughout the day. However, the probability of observing Western Sandpipers, Least Sandpipers, Turkey Vultures, Western Yellowlegs, and Pelagic Cormorants (*Phalacrocorax pelagicus*) increased throughout the day.

Land cover was an also an important predictor for all 71 species. Day of year and day of year squared were significantly ($p < 0.05$) associated with the probability of observing birds for 64 and 59 species, respectively. This indicates that seasonality is an important source of variation in the probability of observing most species included in this analysis. The direction of this effect varies both between and within families. Temperature had a significant effect ($p < 0.05$) on the probability of observing 58 species. Temperature was negatively related to detection of 27 species, across a wide range of taxa, including small aerial insectivores (i.e., Barn Swallow (*Hirundo rustica*), Tree Swallow (*Tachycineta bicolor*)), and diurnal birds of prey (i.e., Bald Eagle, Turkey Vulture). Temperature was positively related to detection of 31 species, also ranging widely in taxa, including waterbirds (i.e., Great Blue Heron, Canada Goose, Mallard (*Anas platyrhynchos*)) and passerines (i.e., Black-capped Chickadee (*Poecile atricapillus*), House Sparrow (*Passer domesticus*)). Precipitation had a significant effect ($p < 0.05$) on the probability of observing 36 species, and the effect was negative for 15 species and positive for 21. This environmental predictor was also important in determining detection of a diverse assortment of species. For example, detection of several passerines was negatively associated with precipitation, including American Robin (*Turdus migratorius*), American Goldfinch, and Dark-eyed Junco (*Junco hyemalis*), yet precipitation was also inversely related to detection of several waterbirds, including Pigeon Guillemot (*Cepphus columba*) and Rhinoceros Auklet (*Cerorhinca monocerata*). The list of species for which precipitation was positively related to detection also included songbirds (i.e., Savannah Sparrow and Common Yellowthroat (*Geothlypis trichas*)) and birds associated with aquatic habitats, including Wood Duck (*Aix sponsa*) and Gadwall (*Mareca strepera*). Complete model results are provided in Appendix C.

3.4 DISCUSSION

Our study shows that ambient concentrations of $PM_{2.5}$, a marker of smoke pollution, during the 2015 – 2018 wildfire seasons affected the probability of observing 26 of the 71 most commonly sighted bird species in Washington, USA. These 26 species included waterbirds, raptors, and passerines, suggesting that $PM_{2.5}$ is an important driver of presence, availability, and/or perceptibility across avian taxa.

Wildfires create and maintain important habitat for birds. For example, some bird species, including woodpeckers and flycatchers, will use early post-fire habitat whereas others, such as the Black-backed Woodpecker (*Picoides arcticus*), are almost entirely dependent on recently burned forests (Hutto, 1995; Saab et al., 2004). While wildfires play a crucial role in generating high quality habitat for some wildlife species, large-scale wildland fires also pose direct threats to animals, including mortality, injury, and health effects from exposure to extreme heat and smoke (Engstrom, 2010). Such health effects may affect bird behaviors, including movement or vocalization. Birds may also adjust their behavior during smoke events in response to cooler air temperatures or reduced visibility. Any behavioral changes exhibited by birds during smoke pollution episodes may affect if and how birds are observed in the wild. Furthermore, impacts of smoke pollution on human observers, such as impaired visibility, may also influence detection of birds. Our results demonstrate a clear impact of $PM_{2.5}$ during the wildfire season on the detectability of birds. Researchers should recognize the potential for smoke and other types of air pollution to affect our observations of birds and other wildlife, which has the potential to change the inferences that might be made in observational studies.

Logically, the effect of air pollution on the probability of observing birds may be especially important during wildfire smoke events, when concentrations of $PM_{2.5}$ are often above air quality standards (Figure 3.3). The average daily concentration of $PM_{2.5}$ for the checklists included in our analysis was 8.6 $\mu g/m^3$ (sd = 14.5 $\mu g/m^3$). However, during smoke events in Washington state between 2015 and 2018, concentrations of $PM_{2.5}$ spiked to well above 150.5 $\mu g/m^3$, the breakpoint between “unhealthy” and “very unhealthy” air quality (Figure 3.1). This is a common occurrence during large-scale wildfires (Laing & Jaffe, 2019). Only 83 checklists included in our analysis were submitted on days when the $PM_{2.5}$ concentration exceeded 150.5 $\mu g/m^3$, highlighting the difficulty of capturing these uncommon events. To ensure that limited availability of bird observations at the most extreme levels of particle pollution did not affect our inference about the species-specific relationship between $PM_{2.5}$ and detection of birds, we ran our models on a subset of our dataset that excluded checklists with $PM_{2.5}$ concentrations above 150.5 $\mu g/m^3$. We found that the relationship between $PM_{2.5}$ and detection of birds remains unchanged for all but one of the 26 species for which we report a statistically significant effect (California Quail). Furthermore, we found that $PM_{2.5}$ became a statistically significant predictor of detection for six additional species, with positive relationships for Steller's Jay, Western Sandpiper, Golden-crowned Kinglet, and Pigeon Guillemot, and negative relationships for Ring-billed Gull and Spotted Sandpiper. None of the species with positive relationships were observed in more than 5 of the 83 checklists with $PM_{2.5}$ concentrations above 150.5 $\mu g/m^3$. This post-hoc analysis highlights the need to collect data on wildlife during poor air quality conditions to better understand species-specific responses, which could be non-linear and may be related to other weather and habitat variables. In fact, $PM_{2.5}$ concentrations vary by land cover, which is another reason why it was important to consider habitat type when assessing the potential effects of $PM_{2.5}$ on detection of birds. It is inherently challenging to collect data on birds and other wildlife during smoke pollution episodes because they are difficult to forecast and often of short duration. We recommend focusing future studies on bird communities within particular habitat types during the wildfire season to better understand how species-specific habitat selection influences avian responses to smoke, especially in landscapes more likely to experience smoke events.

We found that the probability of observing birds was negatively correlated with particle pollution during the wildfire season for 22.5% of the species in our study; however, the probability of observing birds was positively related to $PM_{2.5}$ for some species (14.1%). This suggests that birds exhibit species-specific behavioral changes during air pollution episodes that ultimately influence whether or not they are present and, if so, detected. It is important to note that we could not differentiate whether a bird species was present but not detected or truly absent from a survey location in this analysis. That said, we hypothesized two possible mechanisms that could explain declines in bird observations, specifically: 1) smoke compromised the observational skills of birders (e.g., impaired visibility) or 2) smoke triggered behavioral changes in birds that made them less likely to be observed (e.g., reduced vocalization). We do not expect that poor air quality or limited visibility would enhance a birder's observational skills. Therefore, if the probability of observing birds was driven only by changes in observer ability, we would not expect to find a positive effect of $PM_{2.5}$ for any species. Given that the probability of observing birds increased with elevated concentrations of $PM_{2.5}$ for ten species in our study, our results suggest that at least some species must exhibit behavioral changes during smoke events that make them easier to detect or move into areas that are smoky. We found that species more likely to be observed at higher concentrations of $PM_{2.5}$ included birds often observed in the upper branches of trees, including Cedar Waxwing, Yellow-rumped Warbler, Yellow Warbler, Orange-crowned Warbler, and Western Tanager. If reduced visibility forces these species to forage closer to the ground, they may be more readily observed. Future studies should investigate whether birds use habitat differently during smoke events. Diminished visibility may also prompt birders to focus their attention on species closer to the ground, increasing the probability of observing species often sighted at ground level, such as Spotted Towhee and California Quail.

However, we cannot rule out impaired visibility as a driver of the negative correlation between $PM_{2.5}$ and the probability of observing birds for some study species (Figure 3.3). We expected that smoke impacts on visibility would be most important for birds that are observed at far distances, such as diurnal raptors and gulls. Our results support this notion, as $PM_{2.5}$ was negatively correlated with the probability of observing birds of prey (e.g., Bald Eagle, Red-tailed Hawk, Osprey, Turkey Vulture, Northern Harrier) and gulls (e.g., California Gull, Glaucous-winged Gull (*Larus glaucescens*), Heermann's Gull, and Ring-billed Gull (*Larus delawarensis*)), although this effect did not always meet our threshold for statistical significance (i.e., $p < 0.05$).

Species-specific behavioral responses to wildfire smoke may also explain the inverse relationship between $PM_{2.5}$ and detection of some study species (Figure 3.3). While the presence of observers can affect bird behavior, recent research suggests that this alone does not significantly influence the singing rates of birds (Hutto & Hutto, 2020). Previous research has shown that wildlife acoustic activity may decline during large-scale smoke events following wildfires. Cheyne (2008) reported that gibbons (*Hylobates albibarbis*) do not sing as often when it is smoky and Lee et al. (2017) documented declines in bird vocalization during a prolonged wildfire smoke event. If birds call and sing less during smoke pollution episodes, they may be more difficult to detect in the field. We expected that the probability of observing avian species primarily detected by ear, such as chickadees, kinglets, and other woodland species (Robbins, 1981a), would decline with increasing ambient concentrations of $PM_{2.5}$. Our results suggest that detection of Bushtits decreases at higher concentrations of $PM_{2.5}$ (Figure 3.3); however, $PM_{2.5}$ was not a statistically significant, negative predictor of the probability of observing other woodland species included in this analysis. In addition to reduced vocalization, animals may reduce their activity levels when exposed to toxic particle pollution. Exposure to aerosols has been linked to declines in spontaneous activity (e.g., walking or preening) and reduced water and food intake in rock doves (*Columba livia*) (Sterner, 1993a, 1993b), and a recent study showed that orangutans (*Pongo pygmaeus wurmbii*) are less active during smoke events, resting more and traveling less (Erb et al., 2018).

Less activity could result in lower detection rates. However, racing pigeons exhibited faster homing rates at higher outdoor concentrations of particulate matter (Li et al., 2016). If birds fly faster or spend more time in their territories, they may be more readily detected in and around their activity centers.

While our methods did not allow to us to explicitly test if particle pollution during the wildfire season drives changes in the presence or availability of birds, it is not unreasonable to expect that some avian species may seek refuge from wildfire smoke if they are experiencing severe adverse health impacts. We expected that species with larger home ranges may be better able to emigrate from an area impacted by wildfire smoke pollution than birds with smaller home ranges. Our results support this possibility, as many of the species (e.g., Great Blue Heron, Double-crested Cormorant) that were detected at lower rates with increasing concentrations of $PM_{2.5}$ do have larger home ranges compared to other species analyzed. In addition, smoke degrades visibility and therefore may negatively impact the hunting success of birds of prey, prompting them to relocate. Our results show that the probability of observing several birds of prey, including Bald Eagle, Red-tailed Hawk, Osprey, Turkey Vulture, and Northern Harrier, declined with greater concentrations of $PM_{2.5}$. In the absence of predatorial birds, prey species may be more active and therefore more detectable (MacLeod et al., 2005), which may also explain why the species more readily observed as $PM_{2.5}$ increases includes several smaller songbirds. Future studies should investigate how home range size, territoriality, vigilance, predator-prey dynamics, and daily activity patterns influence behavioral responses to smoke pollution from wildfires.

It is well established that detection and presence of birds are variables that are influenced by temporal and environmental predictors. Migration and breeding phenology drive seasonal patterns in species presence and bird activity (e.g., vocalization), which in turn influences detection

(Skirvin, 1981; Johnson, 2008). To capture how seasonality drives changes in the probability of observing birds, ecologists often include day of year as a linear and quadratic covariate (e.g., Broms et al., 2014; Broms et al., 2016; Purves et al., 2019). We found that day of year and day of year squared were important predictors of the probability of observing 64 and 59 species, respectively, suggesting that seasonality influences detection of a wide range of species. Time of day and weather are also known to have an effect on bird activity (Johnson, 2008). Many bird species are more active in the early morning hours (Robbins, 1981a), which is consistent with our results that show 58 of the 71 study species were more likely to be detected earlier in the day. Some avian species may be less active when exposed to extreme temperatures or during precipitation events (Robbins, 1981b), potentially reducing the probability of observing them. We found that daily average temperature had a significant effect on the probability of observing 58 species whereas precipitation had a significant effect on the probability of observing 36 species, indicating that temperature was overall a more important predictor of detection than precipitation across species included in the analysis.

Our results suggest that for some species, air pollution may be a more important source of variation in the probability of observing birds than standard temporal and environmental predictors such as seasonal variation, time of day, or weather conditions. For example, we found that increased concentrations of $PM_{2.5}$ had a negative effect on the probability of observing Great Blue Herons, and the magnitude of this effect exceeded that of precipitation. Detection of Spotted Towhees was positively related to $PM_{2.5}$, while the effects of both temperature and precipitation on the probability of observing this species were not statistically significant. The effect of $PM_{2.5}$ on detection of Turkey Vultures was more than double the effect of temperature, while precipitation was not a statistically significant predictor of detection for this species.

Our analysis was limited to observations of birds closer to urban areas because we relied on data from the EPA network of ground-based air quality monitors to characterize particle pollution. These monitors are primarily located in cities and towns (Diao et al., 2019; Figure 3.2). Atmospheric models and measurements from satellite instruments could be leveraged to expand the spatial scope of air pollution estimates in future ecological studies, although both approaches have their own limitations that should be carefully considered (Diao et al., 2019). In addition, eBird supports opportunistic data collection, which may result in spatial, temporal, and taxonomic biases (Boakes et al., 2016). Still, our results suggest that, at least in locations near ground-based air quality monitoring sites in Washington where eBirders were active in July, August, and September of 2015 – 2018, detection of 36.6% of the most commonly observed bird species was impacted by outdoor concentrations of $PM_{2.5}$, a marker of smoke pollution. Furthermore, by including year as a categorical predictor in our models we may have underestimated the true effect of $PM_{2.5}$ on the probability of observing birds. We included year to account for annual variation in population demographics that would influence the probability of observing birds; however, year is also a significant predictor of the daily concentration of $PM_{2.5}$ due to annual variation in the frequency and intensity of smoke events (Figure 3.1).

Our study suggests that wildfire smoke may impact the presence, availability, and/or perceptibility of birds, which has major consequences for both ornithological research and avian conservation. Many field studies take place during the summer and fall, months which increasingly overlap with an extended wildfire season and large-scale smoke events. Our model selection results suggested that the top model included $PM_{2.5}$ for over 50% of the species; thus, by not including air quality as a predictor in ecological models, we may be missing an important source of variation in the detection of birds. Failing to model heterogeneity in detection would bias our inference about bird activity and population demographics (Kéry et al., 2010). Occupancy models would be useful in teasing out the effect of wildfire smoke on the perceptibility of birds while accounting for the influence of habitat in determining where species are present. eBird data can be used to build occupancy models, although doing so requires careful consideration of the definition of a site and the covariates used to account for heterogeneity in surveys (Johnston et al., 2019). Targeted sampling before, during, and after wildfire smoke events may be most useful in assessing how smoke affects avian behavior and movement or the detectability of birds. However, air pollution episodes are often unpredictable, and it may be difficult for researchers to capture these events even in the most well-designed studies. Researchers may consider implementing before-after-control-impact studies around prescribed burns as an alternative strategy to characterizing how smoke affects bird behavior, although it is worth noting that the smoke from prescribed burns is less toxic than smoke from wildfires (Prunicki et al., 2019). Avian behavioral responses to particle pollution could signal underlying health effects, serve as effective strategies to limit exposure to toxic gases and aerosols, and/or stem from changes in the physical environment (e.g., visibility) or other stressors (e.g., predators) during smoke events. Regardless, behavioral responses to wildfire smoke may ultimately impact fitness, survival, and reproductive success. Although the long-term health consequences of smoke exposure for wildlife could be substantial (Black et al., 2017), research is limited (Lee et al., 2017; Erb et al., 2018). It is therefore critical to rapidly expand existing knowledge on how animals are affected by wildfire smoke and identify which species may be most at risk.

3.5 CONCLUSION

Our study shows that the ambient concentration of $PM_{2.5}$, a marker of smoke pollution, was an important source of variation in the probability of observing birds in Washington state during the wildfire seasons of 2015 – 2018. Incidence of large-scale wildfire smoke events is expected to increase under future climate change scenarios (Jacob & Winner, 2009); understanding avian behavioral responses to wildfire smoke and how perceptibility of birds changes during smoke events is a critical to inform wildlife research and avian conservation. Finally, our study demonstrates that community science programs could be an important source of data in future studies looking at the impacts of smoke events or other air pollution episodes on birds. We found that eBirders not only survey birds across vast expanses, but they also continued to conduct surveys during large-scale smoke events. Community science data could therefore be a valuable resource for ecologists looking to characterize broad-scale impacts of major pollution events on wildlife populations.

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Chapter 4. LARGE-SCALE BIOACOUSTICS SURVEY DEMONSTRATES IMPACT OF WEATHER, BUT NOT AIR POLLUTION, ON BIOPHONY

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Abstract: Despite the growing popularity of ecoacoustics in wildlife monitoring, few studies have used acoustic indices to investigate how day-to-day changes in weather and air pollution impact biophony, or sounds produced by vocal animals, which could provide valuable insight into how environmental conditions affect the health and behavior of wildlife. We conducted a large-scale bioacoustics survey in two rural study areas in eastern Washington state and evaluated the effects of air temperature, precipitation, and fine particulate matter ($PM_{2.5}$) on four commonly used acoustic indices, including the Acoustic Complexity Index, the Acoustic Diversity Index, the Bioacoustic Index, and the Normalized Difference Soundscape Index. We found that daily temperature and precipitation contributed to diurnal variation in wildlife acoustic activity, whereas $PM_{2.5}$ did not have a statistically significant effect on biophony. Our results demonstrate that acoustic indices can be used to bolster understanding of how daily environmental conditions alter soundscapes and suggest that more research is needed to characterize how weather and air pollution influence biophony. *Keywords:* weather, air pollution, smoke, Acoustic Complexity Index, Acoustic Diversity Index, Bioacoustic Index, Normalized Difference Soundscape Index

4.1 INTRODUCTION

Audio recorders are increasingly used by ecologists to study and monitor wildlife (Browning et al., 2017), including birds (Kirschel et al., 2009; Medina & Francis, 2012), amphibians (Hsu et al., 2006; Xie et al., 2017), and insects (Gasc et al., 2018). New technologies have made recording equipment (e.g., AudioMoth, Solo) more affordable, allowing researchers to collect audio recordings at greater spatial and temporal scales (Browning et al., 2017; Farina, 2018; Xie et al., 2017). Audio recorders collect bioacoustics data, which capture "soundscapes," (i.e., the acoustic environments of specific locations), thereby providing a rich source of information about ecological communities, including the presence, abundance, and behavior of wildlife (Browning et al., 2017; Ozga, 2017). Acoustic ecology, or "ecoacoustics," investigates the biotic and abiotic factors that drive variation in the composition of natural and anthropogenic sounds in soundscapes (Farina & Gage, 2017; Ozga, 2017). Within acoustic ecology, dozens of acoustic indices have been developed to estimate features of audio recordings that relate to specific characteristics of an ecological community (Buxton et al., 2018; Farina & Gage, 2017; Ross et al., 2021). For example, the Acoustic Complexity Index (ACI) was developed to monitor avian singing activity and is highly correlated with the frequency of bird vocalizations (Pieretti et al., 2011). The Bioacoustic Index (BI) has also been used to monitor birds and is highly correlated with avian abundance (Boelman et al., 2007). Other indices were developed to characterize acoustic biodiversity across taxa, such as the Acoustic Diversity Index (ADI), which is based on the Shannon's Diversity Index (Villanueva-Rivera et al., 2011). Others explicitly consider both anthrophony (i.e., human-generated noise) and biophony (i.e., biological noise). For example, the Normalized Difference Soundscape Index (NDSI) represents the ratio of biophony to anthrophony in a soundscape, where higher values indicate a greater proportion of biological noise (Kasten et al., 2012). Acoustic indices such as ACI, ADI, BI, and NDSI have been used to address a number of research objectives (Buxton et al., 2018), including evaluating the impacts of climate change (Buxton et al., 2016) and human activity (Doser et al., 2020) on wildlife communities.

Despite the growing popularity of ecoacoustics in wildlife monitoring, few studies have used acoustic indices to evaluate how day-to-day changes in environmental conditions, such as temperature, precipitation, and air quality, impact biophony. Understanding how weather and air pollution influence the sounds produced by vocal animals provides valuable insight into how such conditions impact the health and behavior of wildlife. For example, studies have shown that the onset of bird dawn chorus can be positively (Puswal et al., 2021) or negatively (Dadwal & Bhatt, 2017; Marín-Gómez & MacGregor-Fors, 2021) related to air temperature. Some birds may begin singing later on rainy days (MacDonald & Islam, 2021; Marín-Gómez & MacGregor-Fors, 2021), and rainfall also increases the calling activity of frogs (Hsu et al., 2006; Xie et al., 2017). Bornean white-bearded gibbons (*Hylobates albibarbis*) sing less when exposed to smoke from wildfires, possibly due to underlying health effects (Cheyne, 2008). If weather or air quality trigger behavioral responses in wildlife that ultimately influence biophony, then we should observe corresponding changes in acoustic indices used to monitor wildlife. For example, Lee et al. (2017) showed that ACI, ADI, BI, and NDSI all decreased as smoke pollution from wildfires increased. They hypothesized that this decline in biophony could have occurred due to reduced animal vocalization, shifts in the timing of wildlife activity, or animal mortality (Lee et al., 2017).

Given the increasing accessibility of audio recorders and greater availability of bioacoustics data, there is tremendous potential for the use of acoustic indices to study wildlife activity under different environmental conditions at large spatial scales. In this study, we used data from a large-scale bioacoustics survey in eastern Washington state during the summer of 2019 to evaluate the effects of weather and air pollution on ACI, ADI, BI, and NDSI. We expected that biophony would be inversely related to temperature, precipitation, and fine particulate matter ($PM_{2.5}$). Our study is the first to examine the impact of both weather and air quality on soundscapes and as such demonstrates the value of considering the effects of multiple, simultaneous environmental conditions on biophony.

4.2 METHODS

4.2.1 *Data Collection*

4.2.1.1 Study Areas

We collected bioacoustics data in two study areas in eastern Washington state in summer 2019 as part of the Washington Predator-Prey Project, a collaboration between the Washington Department of Fish & Wildlife and the University of Washington. The Northeast study area (4,535 km^2) was located in the northeast corner of the state, and the Okanogan study area (5,300 km^2) was located in north-central Washington (Figure 4.1). We deployed AudioMoths (low-cost bioacoustics recorders developed by Open Acoustic Devices) at 87 monitoring sites across both study areas beginning in May 2019. Locations were chosen based on a stratified random sampling design by Bassing et al. (in prep) and represented a wide variety of land cover types on both public and private property. The forests of the Northeast study area are interspersed with shrubland, and elevation ranged from 430 to 1,342 m (median = 839 m) at our monitoring sites. All but one monitoring site in this study area were forested and 10 were located in riparian zones. The Okanogan varies more widely in elevation, from hills in the east to much steeper terrain in the west; elevation ranged from 403 m to 2,041 m at our monitoring sites in this study area (median = 1,174 m). Although the majority of monitoring sites in the Okanogan were forested (79%), this study area also included more open habitat and some developed areas. Seven monitoring sites in the Okanogan were located in riparian zones.

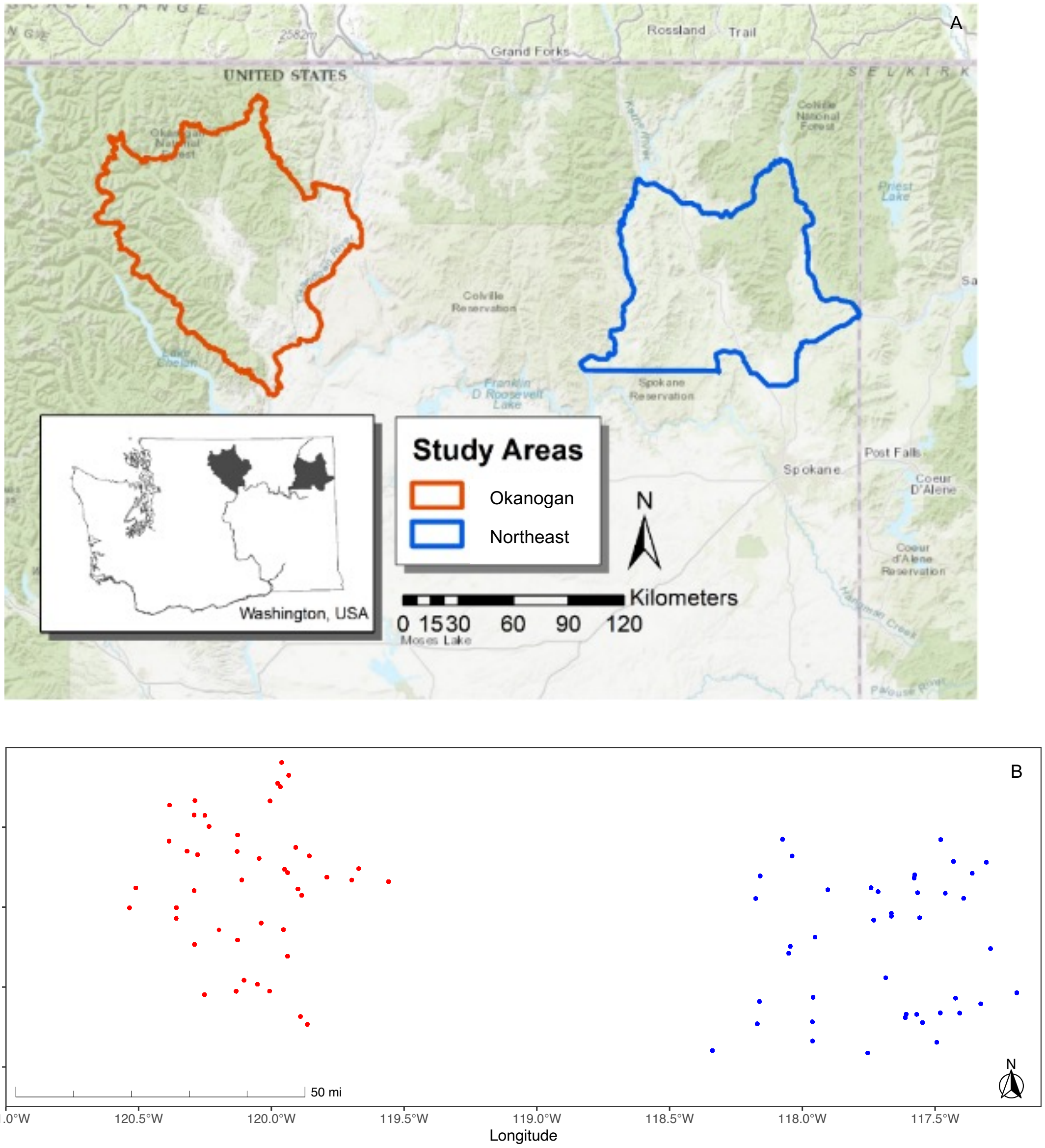

Figure 4.1: Map of a) study areas and b) monitoring sites included in our study. We collected bioacoustics data during July – September, 2019 at 87 monitoring sites in two study areas in eastern Washington state, including 45 sites in the Okanogan study area (red) and 42 sites in the Northeast study area (blue).

4.2.1.2 Audio Recordings

We wanted to capture acoustic activity before and after sunrise; as such, we used several recording schedules to program the AudioMoths to account for shifts in the average sunrise time as the summer progressed. AudioMoths were set to record continuously for 4 to 6 hours each morning. Because these recorders require one minute to write a .wav file for a single hour-long recording, we configured our units to record 60 minutes of audio, then pause for one minute, for the duration of the recording period. All units recorded at a sampling rate of 32 KHz with medium gain, which ensured that we fully captured all animal vocalizations < 16 KHz (Browning et al., 2017). This includes most wildlife species that emit sounds in the audible range. AudioMoths collected data until they ran out of battery; on average, our recorders were active for 233.5 hours. To extend sampling, we replaced units at monitoring sites throughout the summer as time and resources allowed. For our analysis, we focused on recordings collected during July – September and pooled all recordings collected by the AudioMoth(s) deployed at each monitoring site during that period. To reduce the impact our activity in the field may have had on wildlife vocalizations, we excluded recordings collected on days that we conducted fieldwork prior to our analysis.

4.2.1.3 Acoustic Indices

We divided the 1-hour recordings collected in the field into six 10-minute subsamples, then used the *soundecology* package (Villanueva-Rivera & Pijanowski, 2018) in R (R Core Team, 2021) to calculate ACI, ADI, BI, and NDSI for each subsample. For each day in our study period (July 1 – September 30, 2019), we determined the exact sunrise time at each monitoring site and defined the dawn chorus as a window that started two hours before and ended two hours after sunrise. We then computed the mean value of ACI, ADI, BI, and NDSI for each day at each site, using only those subsamples that fell within the dawn chorus. We limited our analysis to days with a minimum of six subsamples.

4.2.1.4 Microhabitat Covariates

We defined the microhabitat at each monitoring site according to 4 variables, as follows. The area immediately surrounding the AudioMoth was classified as either “forested” or “non-forested.” Forested areas included low-elevation and high-elevation mixed coniferous forest and timber stands. Non-forested areas included grassland, sagebrush, and agricultural habitat. In addition, we noted whether the site was in a riparian zone (i.e., a creek or river was visible and/or audible) and estimated the percent canopy cover to the nearest 5% directly above the AudioMoth. Finally, we extracted the elevation for each site from the Shuttle Radar Topography Mission (SRTM) digital elevation model (Farr et al., 2007), which has a spatial resolution of ~ 30 meters.

4.2.1.5 Environmental Covariates

We used data from the North American Regional Reanalysis (NARR), run by the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Prediction (NCEP), to characterize daily weather conditions at each monitoring site. NCEP reanalysis data were provided by the NOAA Physical Sciences Laboratory (PSL) in Boulder, Colorado, USA from their website at https://psl.noaa.gov/data/gridded/data.narr.html. We used the *ncdf4* package (Pierce, 2019) in R (R Core Team, 2021) to extract daily mean air temperature and daily accumulated precipitation for each day at each site included in our analysis. NARR data have a spatial resolution of ~32 kilometers.

We used estimates of $PM_{2.5}$ to capture daily variation air pollution at monitoring sites. $PM_{2.5}$ includes all suspended solid and liquid particles < 2.5 microns in aerodynamic diameter; wildfire smoke is a major source of $PM_{2.5}$ in our study areas. Estimates were extracted from AIRPACT (Air Indicator Report for Public Awareness and Community Tracking), a regional air quality model run by the Laboratory for Atmospheric Research at Washington State University. This integrated meteorological-emissions model predicts the daily mean concentration of $PM_{2.5}$ at a location based on the transformation and transport of emissions from point sources, including wildfires and prescribed burns.

4.2.2 *Statistical Analysis*

We built linear mixed models to estimate the effects of microhabitat, weather, and air quality on ACI, ADI, BI, and NDSI. We fit 8 models, one for each combination of index and study area (e.g., ACI in the Okanogan, ADI in the Northeast, etc.), using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2021). We modeled each index as:

$$transform(INDEX_{i,j}) = \alpha_0 + \alpha_1 * forested_i + \alpha_2 * canopy\ cover_i + \alpha_3 * riparian_i + \alpha_4 * elevation_i + \alpha_5 * day\ of\ year_{i,j} + \alpha_6\ x\ day\ of\ year_{i,j}{}^2 + \alpha_7 * temperature_{i,j} + \alpha_8 * precipitation_{i,j} + \alpha_9\ x\ PM_{2.5_{i,j}} + \in$$

We included several fixed effects to account for differences in habitat across monitoring sites, including elevation, percent canopy cover, and two binary variables that indicated if a site was forested/non-forested (i.e., “forested”) and in/not in a riparian zone (i.e., “riparian”). We also included fixed effects of day of year and day of year squared to account for seasonal changes in wildlife behavior (e.g., breeding, migration) that may have affected vocalization and acoustic activity. To investigate the relationship between environmental conditions and acoustic indices, we included fixed effects of daily mean air temperature, daily accumulated precipitation, and daily mean concentration of $PM_{2.5}$. We allowed the intercept α_0 to vary by site as a random effect to account for additional sources of variation between sampling locations. The residual term is normally distributed such that $\in_i$ ~ Normal(0, σ^2). All continuous covariates were standardized prior to analysis.

Although these acoustic indices are not truly normally distributed variables — ACI, ADI, and BI are nonnegative, and NDSI ranges from -1 to +1 — it is common practice to use a normal distribution to model these indices, on the condition that the data either roughly follow a normal distribution (Khanaposhtani et al., 2019; Mammides et al., 2017; Myers et al., 2019; Pekin et al., 2012) or have been transformed to better meet this assumption (Gasc et al., 2018a; Myers et al., 2019; Raynor et al., 2017). After inspecting model residuals, we decided to transform our data. We used a log transformation for ACI, ADI, and BI. To model NDSI, we used the following transformation, as described by Doser et al. (2020):

$$log\left(\frac{(NDSI + 1)}{(1 - NDSI)}\right)$$

We computed conditional R^2 values using the *performance* package (Lüdecke et al., 2019) in R (R Core Team, 2021) to assess model fit, and we used 95% confidence intervals to determine which fixed effects in our models were statistically significant.

4.3 RESULTS

As expected, we found spatial and temporal variation in ACI, ADI, BI, and NDSI across the Northeast and Okanogan study areas (Figure 4.2). Day of year was the most important predictor of acoustic indices across study areas — all models except the model of ADI in the Northeast included a statistically significant effect of day of year (Table 4.1). ACI, BI, and NDSI in the Northeast and ACI and ADI in the Okanogan increased with day of year. Day of year had a statistically significant, negative effect on BI and NDSI in the Okanogan. Some indices also exhibited a quadratic relationship with day of year, with positive effects observed for ACI, ADI, and BI in the Okanogan and negative effects observed for BI and NDSI in the Northeast.

Most indices were strongly influenced by precipitation (Table 4.1). Precipitation increased ACI and decreased NDSI across both study areas. ADI was negatively related to precipitation in the Northeast, and BI was positively related to precipitation in the Okanogan. Two models included a statistically significant effect of temperature (Table 4.1) — ACI and BI decreased with increases in temperature in the Northeast study area. Only one model included a statistically significant effect of $PM_{2.5}$ (Table 4.1) — NDSI increased as air quality worsened in the Northeast study area.

At least one microhabitat feature was an important predictor of ACI, ADI, and BI in one or both study areas (Table 4.1). NDSI was not related to microhabitat in either the Northeast or the Okanogan. ADI was higher in forested areas than in non-forested areas in the Okanogan, and canopy cover was a statistically significant, negative predictor of ACI in this study area ($p < 0.05$). BI was higher in riparian zones in both the Northeast and the Okanogan; BI also declined with elevation in the Okanogan.

Table 4.1: Summary of model results. Each row represents one of 8 models included in our analysis, identified by acoustic index (ACI, ADI, BI, or NDSI) and study area (Northeast (NE) or Okanogan (OK)). Columns represent fixed effects, including forested, percent canopy cover, riparian, elevation, day of year, day of year squared, daily mean temperature, daily accumulated precipitation, and daily mean concentration of $PM_{2.5}$. Statistically significant ($p < 0.05$), positive effects are noted with a plus sign (+). Statistically significant, negative effects are noted with a minus sign (–). Empty cells indicate that an effect was not significant. Conditional R^2 values for each model are also provided.

	Forested	**Canopy Cover**	**Riparian**	**Elevation**	**Day of Year**	**Day of Year^2**	**Temperature**	**Precipitation**	**$PM_{2.5}$**	**Conditional R^2**
ACI (NE)					+		–	+		0.36
ACI (OK)		–			+	+		+		0.44
ADI (NE)								–		0.33
ADI (OK)	+				+	+				0.42
BI (NE)			+		+	–	–			0.68
BI (OK)			+	–	–	+		+		0.59
NDSI (NE)					+	–		–	+	0.55
NDSI (OK)					–			–		0.55

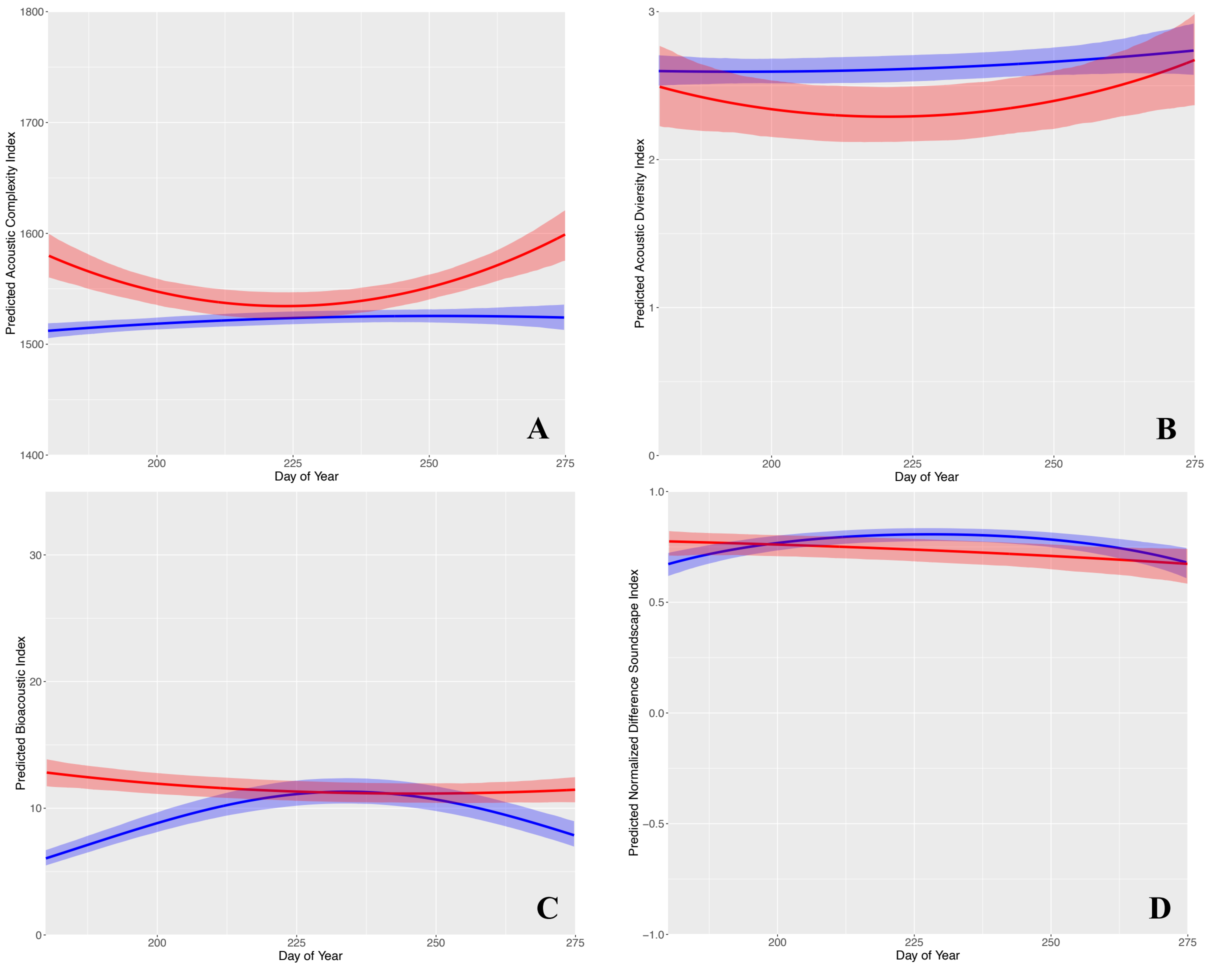

Figure 4.2: Seasonality was an important predictor of acoustic activity in both study areas. Here we show the predicted values of (A) the Acoustic Complexity Index, (B) the Acoustic Diversity Index, (C) the Bioacoustic Index, and D) the Normalized Difference Soundscape Index in forested, non-riparian sites in the Okanogan (red) and Northeast (blue) study areas from day 180 to day 275 in the calendar year, assuming average levels of all other predictors. Solid lines indicate median predictions and ribbons illustrate bootstrapped 95% confidence intervals.

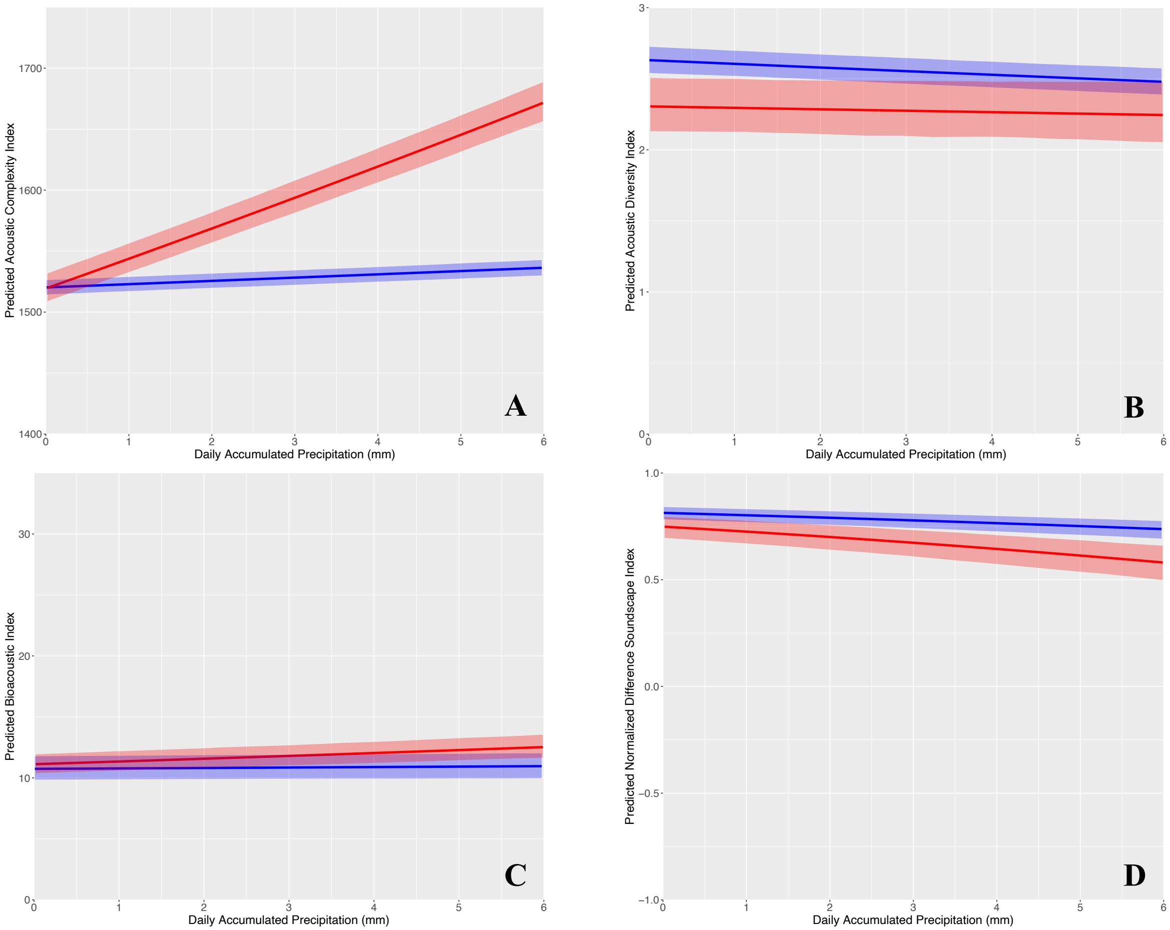

Figure 4.3: Rainfall influenced acoustic activity in both study areas. Here we show the predicted values of (A) the Acoustic Complexity Index, (B) the Acoustic Diversity Index, (C) the Bioacoustic Index, and D) the Normalized Difference Soundscape Index in forested, non-riparian sites in the Okanogan (red) and Northeast (blue) study areas as daily accumulated precipitation increased from 0 to 6 mm, assuming average levels of all other predictors. Solid lines indicate median predictions and ribbons illustrate bootstrapped 95% confidence intervals.

4.4 DISCUSSION

Our study demonstrates that air temperature and precipitation contribute to daily variation in acoustic indices and suggests that ecoacoustics analyses offer a valuable tool for understanding the impacts of multiple environmental conditions on biophony. In fact, our study shows that daily weather conditions may be more important drivers of wildlife acoustic activity than fine-scale differences in habitat — whereas at least one microhabitat variable (i.e., forested, riparian, percent canopy cover, elevation) was statistically significant in 4 of our 8 models, air temperature and/or precipitation were statistically significant predictors in 7 of the 8 models included in our analysis (Table 4.1).

Precipitation drove variation in all 4 acoustic indices in at least one study area (Figure 4.3). As we expected, both ADI and NDSI were inversely related to precipitation. These findings suggest that both acoustic biodiversity and the proportion of biophonic sounds in audio recordings decreased on days with more total rainfall. We expected that precipitation would also be inversely related to ACI and BI because some birds are known to vocalize less frequently when it rains (Lengagne & Slater, 2002; Mennill, 2014). However, we found a positive relationship between precipitation and these two measures of biophony. Taken together, these findings suggest that whereas wildlife acoustic activity across taxa declined on rainy days in our study areas, bird singing activity actually increased. We found that temperature also influenced biophony. In the Northeast, both ACI and BI were negatively related to temperature, which suggests that bird singing activity declined in the Northeast as temperatures rose. However, we did not observe the same relationship between temperature and these two indices in the Okanogan. We believe this could be because birds find heat more tolerable in the Okanogan, likely due to a difference in habitat between the two study areas that we did not fully account for in this analysis.

Air quality was excellent in both the Northeast and the Okanogan during summer 2019 — in fact, the daily mean concentration of $PM_{2.5}$ did not exceed the health-based standard set by the Environmental Protection Agency (EPA) on any days at any monitoring sites included in our analysis. As such, we were not surprised that $PM_{2.5}$ was not an important predictor of biophony in most models. We expect that the relationship between $PM_{2.5}$ and wildlife acoustic activity may be different if our study areas had been impacted by a large-scale wildfire smoke event (Lee et al., 2017); in an analysis of eBird data, Sanderfoot & Gardner (2021) showed that $PM_{2.5}$ impacted the probability of observing birds during the 2015 – 2018 wildfire seasons in Washington state, which suggests that acoustic indices may also change in response to smoke pollution.

Given the annual life history cycle of many animals, we expected to observe seasonality across all four acoustic indices. However, we were surprised to see that the statistical significance and directionality of the fixed effects of day of year and day of year squared differed between the two study areas. These results suggest that although both study areas are located at similar latitudes in the Okanogan ecoregion, seasonal patterns in wildlife and human activity may differ widely between the mixed coniferous forests in northeastern and north-central Washington.

Both of our study areas were located in rural areas dominated by mixed coniferous forest, yet they provided different microhabitats for wildlife (Figure 4.1). This afforded a unique opportunity to explore how fine-scale differences in habitat across two large study areas influence soundscapes. We found that ADI was higher at forested sites in the Okanogan, yet percent canopy cover had a statistically significant, negative effect on ACI in this study area. This suggests that whereas forested areas were positively associated with biodiversity, the frequency of bird vocalizations decreased as canopy cover increased. This could be because some species preferred to sing in more open habitat or because bird vocalizations were absorbed by dense vegetation (Bateman et al., 2021). In addition, we found that elevation was negatively related to BI in the Okanogan, which indicates that there were fewer birds at higher elevations in this study area. We also found that BI was higher at sites located in riparian zones in both the Northeast and Okanogan, which suggests that birds were attracted to microhabitats near water.

4.5 CONCLUSION

Our study illustrates the potential for acoustic indices to help disentangle the effects of multiple environmental conditions on biophony. In addition, we show that the relationships between biophony and microhabitat, temperature, precipitation, and air quality can vary widely, even between two study areas in the same ecoregion. This underscores the need to consider fine-scale variation in wildlife activity, particularly when making predictions about wildlife communities that have yet to be observed. As climate change drives shifts in weather patterns (Stott, 2016) and worsens air pollution in many parts of the world (Clay & Muller, 2019; Jacob & Winner, 2009), it is increasingly important to understand how biophony varies under different environmental conditions and consider what such relationships suggest about underlying impacts on wildlife health and behavior. We recommend that future studies leverage existing archives of bioacoustics data to further explore the effects of weather, air pollution, and other environmental conditions on biophony at large spatial scales.

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Chapter 5. COVID-19 LOCKDOWNS AFFECTED DETECTION OF BACKYARD BIRDS AND AVIAN HABITAT USE IN URBAN AREAS

Publication history: This study was co-authored with Joel D. Kaufman and Beth Gardner. At the time this dissertation was published, a version of this chapter was in review at *Scientific Reports*.

Abstract: During the “Anthropause,” we launched a large-scale community science project to monitor birds in cities in the Pacific Northwest during COVID-19 lockdowns. We expected that lockdowns would drive shifts in human activity, air, and noise pollution — all of which could affect the detection and distribution of birds. We used data collected by 376 volunteers at 429 monitoring sites in Washington and Oregon to investigate how lockdowns in the spring of 2020 influenced site use by and detection of 46 avian species. We found that human activity — as measured by the percent change in human mobility — affected the probability of detecting 76% of study species. Furthermore, 50% of study species were more likely to be detected as human mobility increased. This suggests that these species were detected more often as lockdown restrictions eased, possibly because they used sites monitored by volunteers (namely urban and suburban backyards) more often. We also show that air pollution influenced detection of 22% of study species. Land use was a more important predictor of site use than bird feeders or bird baths across study species. Species-specific responses were highly variable, underscoring the complexity of bird distributions at fine spatial scales in urban areas. *Keywords:* Anthropause,

human mobility, traffic, urban air pollution, fine particulate matter, bird feeders, bird baths, eBird, occupancy

5.1 INTRODUCTION

At the height of the first wave of the COVID-19 pandemic in early April 2020, more than 50% of the world's population was under some type of lockdown, or shelter-in-place order, and vehicle traffic, air travel, and shipping activity plummeted (Bates et al., 2020). This sudden, rapid decline in human mobility is now referred to as the "Anthropause" (Rutz et al., 2020). Changes in human behavior during the Anthropause inevitably influenced the behavior and distributions of wildlife species, especially in more densely populated urban areas where the impacts of COVID-19 lockdowns on daily life were most extreme. The Anthropause therefore provided a unique opportunity to study wildlife responses to abrupt changes in human behavior (Rutz et al., 2020) and explore how elements of urbanization that are often confounded along the urban-to-rural gradient affected wildlife populations. Birds are readily observed in cities and are known to use a wide variety of habitats in developed areas; consequently, investigating the presence and detection of birds in cities during COVID-19 lockdowns serves as a useful case study on the impacts of human activity on urban wildlife.

Avian species avoid, adapt, or exploit urban areas (Blair, 1996), influencing bird distributions and community composition. Many aspects of urbanization are known to affect avian health, behavior, distribution, and/or demography, including percent impervious surface (Lussier et al., 2006), noise pollution (Nemeth & Brumm, 2010; Nemeth et al., 2013; Senzaki et al., 2016), and air pollution (Liang et al., 2020; Sanderfoot & Holloway, 2017). However, quantifying the individual and collective effects of these variables on birds is inherently challenging because they are often correlated. Shifts in a subset of these variables during the

Anthropause, such as noise (Basu et al., 2021; Lecocq et al., 2020; Terry et al., 2021; Venter et al., 2020) and air pollution (Archer et al., 2020; Jiang et al., 2020; Shi et al., 2021), created a rare opportunity to tease out how elements of urbanization influence avian habitat use and detection of birds in cities.

Newfound or renewed interest in outdoor recreation and hobbies during COVID-19 lockdowns may have also impacted birds in urban areas. For example, bird enthusiasts spending more time at home during lockdowns may have been more invested in providing supplementary food or maintaining water features for local wildlife. In addition, restrictions during COVID-19 lockdowns impacted where people could recreate outdoors. As some city, state, and national parks limited visitation or closed entirely, human activity increased in local green spaces not subject to such regulation (Bates et al., 2020). This may have changed how birds utilized urban habitat in the spring of 2020.

During the Anthropause, we launched a community science project in the spring of 2020 to monitor birds in cities under lockdown across the Pacific Northwest. Volunteers signed up to conduct weekly surveys of birds during a data collection campaign beginning April 1st and ending June 30th. More than 900 people enrolled in the program; together, their observations constitute a valuable dataset of bird counts from repeated surveys at hundreds of locations, with most monitoring sites located in major metropolitan areas. Here, we combine this unique community science dataset with data on land use, weather, air pollution, and human mobility to explore how avian species are using the urban-suburban matrix. In addition, we explored how anticipated changes in urban habitat during COVID-19 lockdowns, such as reduced human activity, affected detection of birds. Our goal was to explore how fine-scale spatial and temporal variation in urban habitat contribute to trends in the distributions and detectability of birds in cities and document shifts in bird observations during COVID-19 lockdowns.

5.2 METHODS

5.2.1 *Data Collection*

5.2.1.1 Data Collection Campaign

Volunteers signed up to monitor birds in their neighborhoods beginning April 1st, 2020. We enrolled volunteers on a rolling basis; at the end of our data collection campaign, we had received 917 responses to our online sign-up form. Participants selected their own monitoring sites, and we encouraged volunteers to survey birds on their own property or at a local green space they could safely access while following public health guidelines and without violating shelter-in-place orders. We asked volunteers to conduct 10-minute, stationary point counts at their chosen site at least once a week, from April 1st through June 30th. They recorded all the birds they detected during a point count, using both visual and auditory cues, and submitted their observations from each survey as a complete checklist to eBird, an online database run by the Cornell Lab of Ornithology. eBird supports opportunistic data collection by birders who use a web application to submit checklists of species they observe and information about where and when observations took place (e.g., date, time; Sullivan et al., 2009). To help us identify checklists submitted as part of our data collection campaign in the eBird database, we asked volunteers to flag their checklists by adding the phrase “social distancing survey” to the trip comments field.

5.2.1.2 Volunteer Questionnaire

In July 2020, we invited adult volunteers to participate in an online questionnaire to collect more information about their monitoring sites and their motivations for volunteering. This questionnaire allowed us to collect data on site characteristics that could not be assessed using publicly available datasets, including whether seed or suet feeders, hummingbird feeders, and/or bird baths were made available to birds at survey locations. We received responses from 284 volunteers. All methods were carried out in accordance with relevant guidelines and regulations, including guidelines for human subjects research. Our protocol and questionnaire were reviewed by the Human Subjects Division at the University of Washington (IRB ID: STUDY00010577) and determined to be exempt from a requirement for informed consent.

5.2.1.3 Bird Observations

We downloaded all bird observations from checklists submitted in the U.S. states of Washington, Oregon, California, and Idaho, and British Columbia, Canada from April 1 – June 30, 2020 from the eBird database. To identify those checklists belonging to volunteers in our study, we searched for some variation of the "social distancing survey" flag in the trip and/or species comments and then matched the observer IDs associated with those checklists to the names of our volunteers. We also used auxiliary information collected in the volunteer questionnaire to ascertain the IDs of any volunteers who did not flag their checklists in eBird. We were ultimately able to determine the observer IDs of 431 volunteers. Next, we filtered the bird observations using the *auk* package (Strimas-Mackey et al., 2018) in R (R Core Team, 2020). We only included observations from checklists submitted by volunteers that met our survey protocol (i.e., complete, stationary surveys that were 9 to 11 minutes in duration).

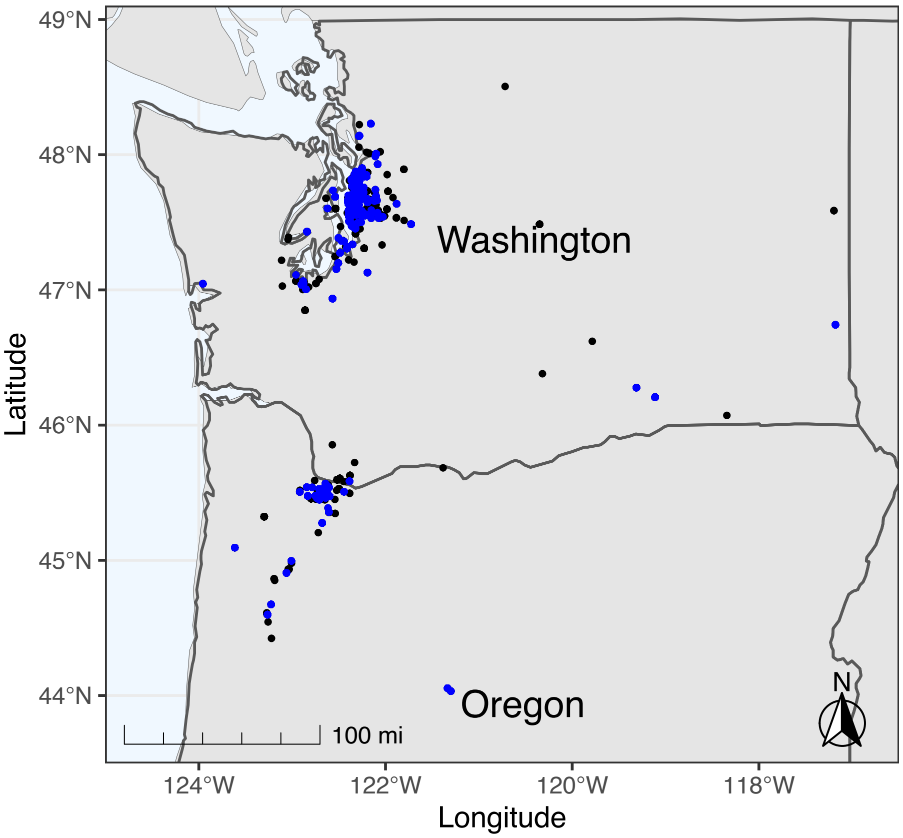


Figure 5.1: Map of study area, which includes the states of Washington and Oregon. Dots mark the locations of all monitoring sites included in our analysis. We had information on supplementary resources (i.e., availability of bird feeders and bird baths) for monitoring sites shown in blue.

Finally, we binned checklists into circular, spatial units with a 100-meter radius using a hierarchical clustering approach implemented using the *stats* package in R. We considered each unit to be a unique site in our analysis. Therefore, all checklists assigned to a site represent surveys that took place within 100 m of the site's center. Sites were heavily concentrated in major metropolitan areas in Washington and Oregon (e.g., Seattle, Portland); we therefore decided to focus our analysis on bird observations from just these two states (Figure 5.1).

There were a total of 193 species observed by volunteers. We chose the species for this study based on the frequency and spatial distribution of detections. We focused on analyzing species that were observed at a minimum of 5% of monitoring sites on at least 150 sampling occasions to ensure that we had sufficient data to fit occupancy models. Forty-six species met these criteria.

5.2.1.4 Environmental Data

We used data from ground-based instruments included in the Environmental Protection Agency (EPA) Air Quality System (AQS) to characterize air pollution at monitoring sites, specifically the ambient concentration of fine particulate matter ($PM_{2.5}$). $PM_{2.5}$ includes all suspended solid and liquid particles smaller than 2.5 microns in aerodynamic diameter. Source apportionment studies show that human activity is an important driver of $PM_{2.5}$ in urban areas, with vehicle traffic accounting for 24% of total $PM_{2.5}$ in U.S. cities (Karagulian et al., 2015). Due to the potentially complex relationships between urban air pollution and weather in cities (Ito et al., 2007), we chose to consider only one pollutant in our analysis. We focused on $PM_{2.5}$ because we felt more confident assessing temporal variation in this pollutant across our study area, as measurements were available from a greater number of instruments. We averaged the daily mean concentration of $PM_{2.5}$ ($\mu g/m^3$) across all sensors within Core-Based Statistical Areas (CBSAs; metro- or micropolitan statistical areas, or areas associated with at least one urban cluster with a minimum population of 10,000) for which a complete time series was available. This allowed us to capture temporal variation in $PM_{2.5}$ within metropolitan and micropolitan areas. We determined the daily mean concentration of $PM_{2.5}$ on the days surveys were conducted, based on the CBSA associated with the monitoring site. We excluded surveys from monitoring sites outside CBSAs, limiting our analysis to metro- and micropolitan areas.

To characterize shifts in human activity during lockdowns, we relied on data from Google LLC's Community Mobility Reports (Google LLC, 2020). These reports provide information on the daily percent change in human mobility across various place categories from a baseline established in the weeks just prior to the pandemic, between January 3rd and February 6th, 2020. Data are available at the county scale. We used data from Waze (Waze, 2020) to compare the percent change in traffic volume to the percent change in human mobility across various place categories in cities in our study area. We chose to use data on human mobility from the "retail and recreation" place category in our analysis because this time series was most highly correlated with that for traffic volume ($r^2 = 0.95$), and we wanted to characterize the impact of reduced traffic during lockdowns on bird observations. The high correlation between the percent change in human mobility and percent change in traffic volume allowed us to consider the former to be a proxy measurement of the latter when interpreting our results.

We used data from the North American Regional Reanalysis (NARR) to capture variability in weather across surveys. We used the *ncdf4* package (Pierce, 2019) in R (R Core Team, 2020) to extract daily mean air temperature and daily accumulated precipitation for each survey. NARR data were provided by the National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Laboratory in Boulder, Colorado, USA from their website at https://psl.noaa.gov/data/gridded/data.narr.html.

To account for differences in habitat across monitoring sites, we extracted data on land cover and percent canopy cover from the 2016 National Land Cover Database (NLCD), developed by the Multi-Resolution Land Characteristics (MRLC) Consortium, in ArcMap (Esri, 2019; Esri Inc., 2020). Land cover classifications were grouped into three categories: highly developed (more than 50% impervious surface), low developed (less than 50% impervious surface), and natural areas (forest, shrubland, wetland, etc.). We obtained information on supplementary resources available to birds at monitoring sites from the online questionnaire administered to volunteers (see above). We used responses from volunteers to build three binary, categorical variables to indicate availability of seed or suet feeders, hummingbird feeders, and/or bird baths at monitoring sites.

5.2.2 *Statistical Analysis*

We created survey-by-site detection histories for each monitoring site and all 46 species included in the dataset. We analyzed these detection/non-detection data using single-season occupancy models, fit using the *unmarked* package (Fiske & Chandler, 2011) in R (R Core Team, 2020). Occupancy models are commonly used by ecologists to explore bird distributions because they allow researchers to account for imperfect detection (i.e., the possibility of failing to detect a species, even though it is present). We defined the season as the duration of the data collection campaign (April 1 – June 30, 2020), which aligns with the breeding season for many study species.

In addition to the covariates described above, we included a few additional effects to account for how seasonal and daily variation in bird activity influenced detection of birds. We included day of year and day of year squared as predictors of detection, knowing that the probability of observing birds may vary seasonally and this temporal variation may be linear or quadratic. We also included an indicator variable for whether a survey was conducted on a Saturday or Sunday to account for differences in human activity on weekends. To adjust for the daily activity patterns of birds, we included time of day and time of day squared as covariates on detection. A correlation matrix for the numeric effects on detection is included in Appendix E. For each of the 46 study species, we modeled ψ_i, the probability that a species was present at monitoring site i as:

$$logit(\psi_i) = \alpha_0 + \alpha_1 * land\ cover_i + \alpha_2 * canopy\ cover_i$$

We modeled p_{ij}, the probability of detecting a species at site i in survey j as:

$$\begin{aligned} logit(p_{ij}) = \beta_0 + \beta_1 * day_{ij} + \beta_2\ x\ day_{ij}{}^2 + \beta_3\ x\ weekend_{ij} + \beta_4\ x\ time_{ij} + \beta_5\ x\ time_{ij}{}^2 \\ + \beta_6\ x\ temperature_{ij} + \beta_7\ x\ precipitation_{ij} + \beta_8\ x\ mobility_{ij} \\ + \beta_9\ x\ PM_{2.5_{ij}} \end{aligned}$$

We used 95% confidence intervals to determine which effects were statistically significant.

Occupancy models typically rely on a clear delineation of a site; however, this can be difficult to determine in contiguous habitat and particularly when comparing species for which home range sizes vary widely. Given that home ranges of study species may exceed the size of monitoring sites, species may not be constantly present within a site. Consequently, we interpreted the probability of occupancy (ψ) as the probability of use. Covariates on ψ therefore represent effects on site use, providing insight into what makes sites within urban areas attractive to birds. The probability of detecting birds (p) reflects both the probability that a species is available at a site during a survey and the probability that it is then perceived by an observer. Therefore, effects on p may be due to shifts in avian behavior that impact the visual and/or auditory cues relied on by observers (e.g., movement, vocalization) or survey conditions that influence perceptibility (e.g., visibility, background noise; Johnson, 2008).

We also conducted a secondary analysis to investigate whether provision of supplementary resources attracted birds to monitoring sites. In this analysis, we considered the effects of bird feeders, hummingbird feeders, and bird baths on species presence in addition to the variables included in the equation provided above.

5.3 RESULTS

Our final dataset included observations of 46 species from 6,640 eBird checklists submitted by 376 unique observers at 429 monitoring sites (Figure 5.1). We found that both human mobility and air pollution affected the probability of detecting birds in cities during COVID-19 lockdowns in the Pacific Northwest. Human mobility gradually increased across the region during the data collection campaign as lockdown restrictions were lifted (Figure 5.2). The percent change in human mobility had a statistically significant effect on the detection of 35 of the 46 study species (76%). As the percent change in human mobility increased, 12 species were less likely to be detected and 23 species were more likely to be detected. No clear pattern was observed among these species with respect to their diet, foraging strategy, use of vertical space, or level of synanthropy (Table 5.1). $PM_{2.5}$ had a statistically significant effect on detection of 10 of the 46 study species (22%) (Table 5.1).

We also found that land cover was a statistically significant predictor of occupancy for 22 of the 46 study species (48%), including suburban adapters and urban exploiters. Canopy cover was a statistically significant predictor of presence for 9 study species (20%) (Table 5.1). As expected, seasonality, time of day, and weather affected the probability of detecting a wide range of species. Day of year and day of year squared had a statistically significant effect on the probability of detecting 29 and 22 species (63% and 48%), respectively. Weekends influenced the probability of detecting 5 species (11%). Time of day had a statistically significant effect on the detection of 65% of study species (30 total), and time of day squared had a statistically significant effect on detection of 54% of study species (25 total). Temperature influenced detection of 13 species (28%), and precipitation influenced detection of 9 species (20%) (Table 5.1). Complete model results are provided in Appendix F.

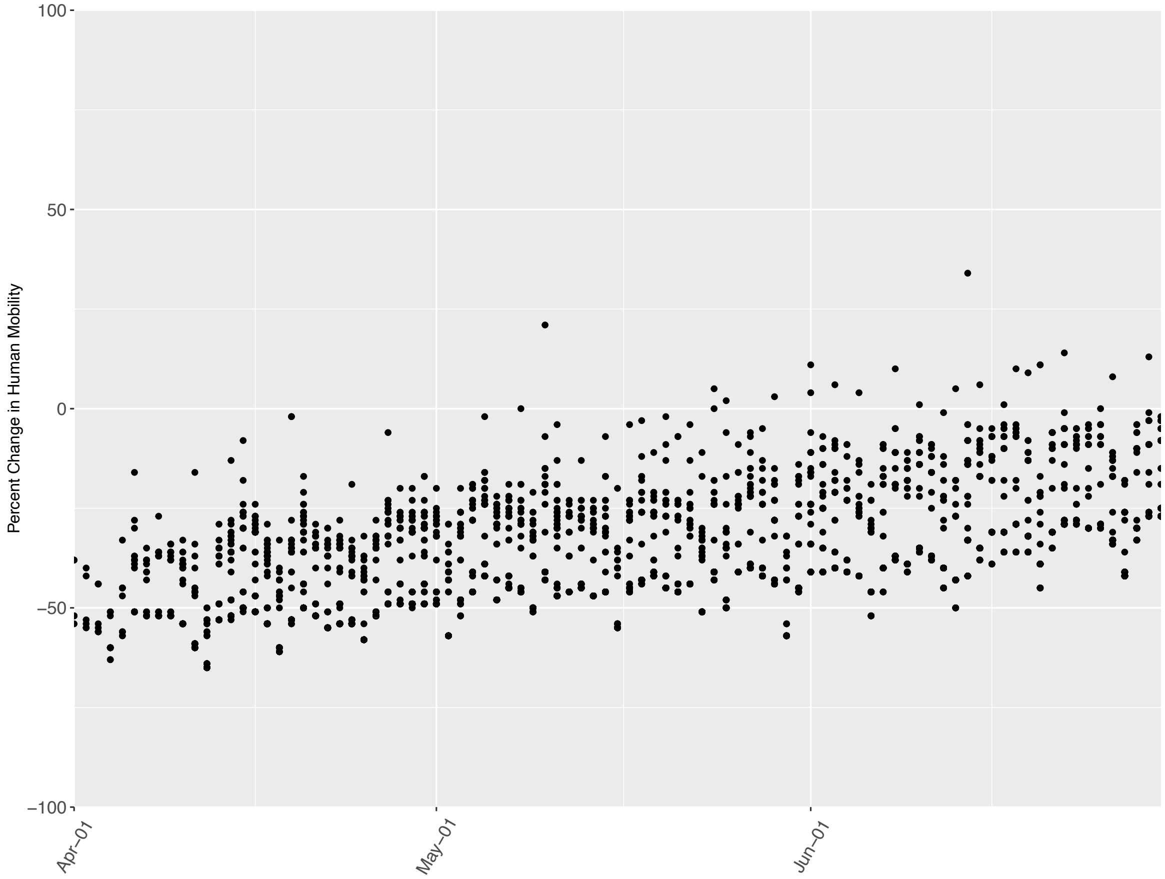
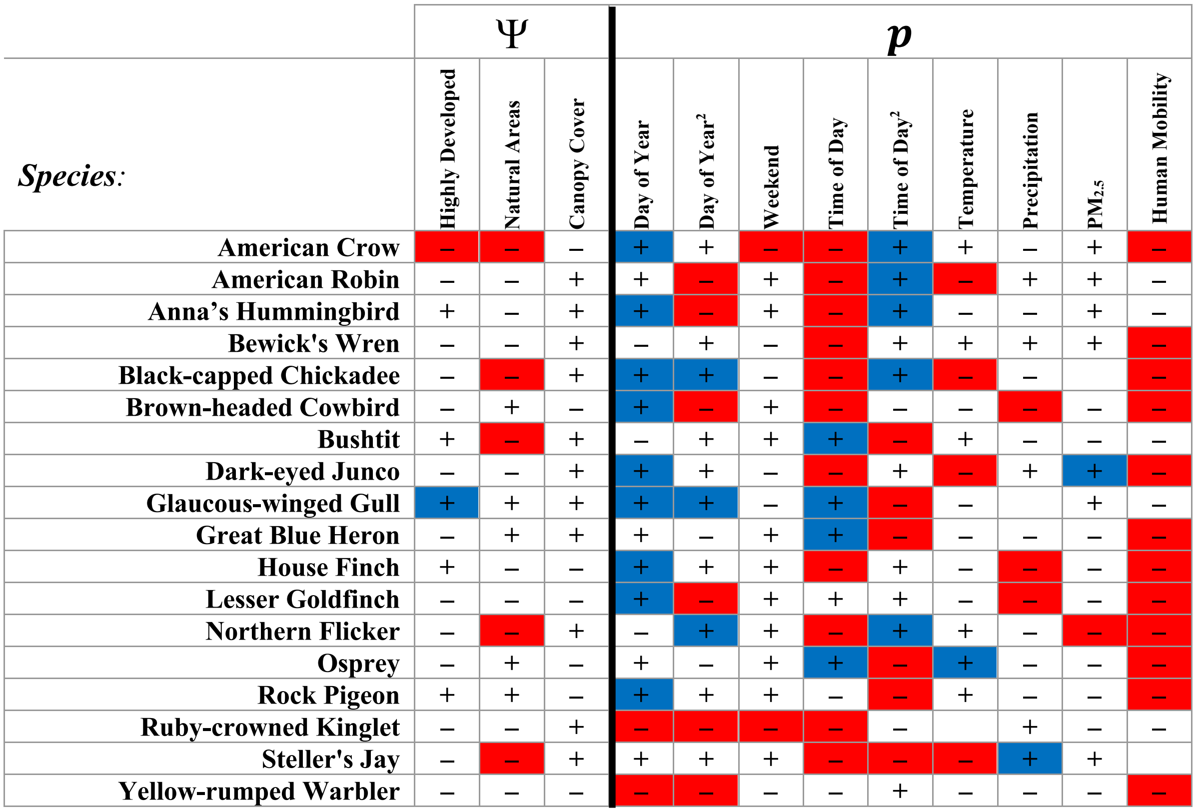


Figure 5.2: Percent change in daily human mobility relative to a pre-pandemic baseline at monitoring sites during the data collection campaign. Negative values indicate that human mobility was lower than it was before the pandemic. Note that human mobility was suppressed across the study area during COVID-19 lockdowns.

Table 5.1: Results of single-season occupancy models by species. The top panel includes results for species that were less likely to be detected at higher levels of human mobility, and the bottom panel includes results for species that were more likely to detected at higher levels of human mobility. The first three covariates (including highly developed, natural areas, and canopy cover) were included as predictors of occupancy in all models. The next nine covariates (including day of year, day of year squared, weekend, time of day, time of day squared, temperature, precipitation, $PM_{2.5}$, and human mobility) were included as predictors of detection. Blue boxes indicate statistically significant, positive effects ($p < 0.05$), and red boxes indicate statistically significant, negative effects. Empty boxes indicate effects with coefficient estimates of zero. Complete model results are provided in Appendix F.



	Ψ			***p***								
***Species*:**	**Highly Developed**	**Natural Areas**	**Canopy Cover**	**Day of Year**	**Day of Year^2**	**Weekend**	**Time of Day**	**Time of Day^2**	**Temperature**	**Precipitation**	**$PM_{2.5}$**	**Human Mobility**
American Crow	–	–	–	+	+	–	–	+	+	–	+	–
American Robin	–	–	+	+	–	+	–	+	–	+	+	–
Anna’s Hummingbird	+	–	+	+	–	+	–	+	–	–	+	–
Bewick's Wren	–	–	+	–	+	–	–	+	+	+	+	–
Black-capped Chickadee	–	–	+	+	+	–	–	+	–	–		–
Brown-headed Cowbird	–	+	–	+	–	+	–	–	–	–	–	–
Bushtit	+	–	+	–	+	+	+	–	+	–	–	–
Dark-eyed Junco	–	–	+	+	+	–	–	+	–	+	+	–
Glaucous-winged Gull	+	+	+	+	+	–	+	–	–		+	–
Great Blue Heron	–	+	+	+	–	+	+	–	–	–	–	–
House Finch	+	–	–	+	+	+	–	+	–	–	–	–
Lesser Goldfinch	–	–	–	+	–	+	+	+	–	–	–	–
Northern Flicker	–	–	+	–	+	+	–	+	+	–	–	–
Osprey	–	+	–	+	–	+	+	–	+	–	–	–
Rock Pigeon	+	+	–	+	+	+	–	–	+	–	–	–
Ruby-crowned Kinglet	–	–	+	–	–	–	–	–		+	–	–
Steller's Jay	–	–	+	+	+	+	–	–	–	+	+	
Yellow-rumped Warbler	–	–	–	–	–	–	–	+	–	–	–	–

	Ψ			*p*								
***Species**:*	**Highly Developed**	**Natural Areas**	**Canopy Cover**	**Day of Year**	**Day of Year^2**	**Weekend**	**Time**	**Time^2**	**Temperature**	**Precipitation**	**PM$_{2.5}$**	**Human Mobility**
American Goldfinch	–	+	–	–	+	+	–	–	+	–	–	+
Bald Eagle	–	+	–	–	–	+	+	–	–	–	+	+
Band-tailed Pigeon	–	+	+	+	–	–	–	–	–	+	+	+
Barn Swallow	–	+	–		–	+	+		+	+	–	+
Black-headed Grosbeak	–	+	+	+	–	+	+	–	+	+	+	+
California Scrub-jay	+	+	–	–	+	+	–	–	–	–	–	+
Canada Goose	–	+	–	–	+	–	+	–	+	–	–	+
Chestnut-backed Chickadee	–	–	+	+	+	–	+	–	–	+	+	+
Downy Woodpecker	–	–	+	–	+	+	–	–	+	+	–	+
Eurasian Collared-Dove	–	+	–	–	+	+	–	–	+		–	+
European Starling	+	+	–	–	–	+	–	+	+	+	–	+
Golden-crowned Kinglet	+	–	+	–	–	–	+	–	–	+	+	+
Golden-crowned Sparrow	–	–	–	–	–	+	–	–	–	+	+	+
House Sparrow	+	–	–	–	+	+	+	+	+	–	–	+
Mallard	–	+	–	–	+	+	+	–	+	+	+	+
Mourning Dove	–	+	–	–	+	+	–	–	+	–	–	+
Orange-crowned Warbler	+	–	–	–	–	–	–	+	–	–	–	+
Pine Siskin	–	–	+	–	–	–	+	–	+	+	–	+
Purple Finch	–	+	+	–	–	+	–	+	+	–	+	+
Red-breasted Nuthatch	–	–	+	+	+	–	–	–		+	+	+
Red-winged Blackbird	–	+	–	–	–	+	+	–	+	+	+	+
Rufous Hummingbird	–	+	–	+	–	–	+	+	–		+	+
Song Sparrow	–	–	+	–	+	+	–	+	–	+	–	+
Spotted Towhee	–	–	+	–	–	–	–	+	–	+	+	+
Tree Swallow	–	+	–	–	–		+	–	+	+	–	+
Violet-green Swallow	–	+	+	–	–	–	+	+	–	–	+	+
White-crowned Sparrow	+	+	–	–	+	+	–	–	+	+	–	+
Wilson's Warbler	+	–	+	–	–	+	–	+	–	–	–	+

We conducted a secondary analysis on a subset of surveys for which we had additional information on availability of feeders and bird baths. Some volunteers chose not to participate in our online questionnaire, so information on supplementary resources was not available for every monitoring site, limiting this analysis to 5,459 surveys from 248 observers at 242 monitoring sites. Our secondary analysis showed that provision of supplementary resources also influenced species presence. Four species (9%) were more likely to be present at sites with seed or suet feeders, and 5 species (11%) were less likely to be present at sites with seed or suet feeders.

Anna’s Hummingbird (*Calypte anna*) and Rufous Hummingbird (*Selasphorus rufus*) both showed strong, positive associations with the availability of hummingbird feeders. Finally, 6 of the 46 study species (13%) were more likely to be present at sites with bird baths; no species were negatively associated with this resource.

5.4 DISCUSSION

During the Anthropause, we successfully launched a large-scale community science project which provided data from thousands of bird surveys conducted across the Pacific Northwest during COVID-19 lockdowns. The results from this study demonstrate that birds respond to multiple characteristics of urban habitat, including human activity, air pollution, land use, and provision of supplementary resources. Species-specific responses across this set of biotic and abiotic factors are highly variable, underscoring the complexity of bird distributions at fine spatial scales in urban areas. Our study also illustrates the value of community science and shows that volunteer-collected data may be leveraged to assess the impact of sudden, extreme events on birds.

We found an intriguing and unexpected relationship between human mobility and detection of birds. In our study area, the percent change in human mobility (Figure 5.2) was highly correlated with traffic volume. As such, a decline in human mobility meant fewer cars on the road, likely leading to reductions in noise pollution. Research has shown that background noise reduces the detectability of birds (Pacifici et al., 2008); we therefore expected that human mobility would either be inversely related to the probability of detecting birds or have no effect on detection. Instead, we found that human mobility had a statistically significant, positive effect on the probability of detecting 50% of study species and a statistically significant, negative effect on the probability of detecting 26% of study species. This suggests that human mobility in urban areas influences the detectability of a wide range of species; in fact, human mobility was the single most important environmental predictor of detection across our study species, influencing detection of a greater proportion of species than temperature, precipitation, or $PM_{2.5}$. We observed positive effects of human mobility on detection for a diverse assortment of species that vary widely in terms of diet, behavior, and level of synanthropy (i.e., degree of association with humans) (Table 5.1); contrary to our expectations, several species that we commonly detect by ear in the field were observed more readily at greater levels of human mobility, including American Goldfinch (*Spinus tristis*), Pine Siskin (*S. pinus*), Red-breasted Nuthatch (*Sitta canadensis*), Song Sparrow (*Melospiza melodia*), and White-crowned Sparrow (*Zonotrichia leucophrys*).

These results demonstrate that the relationship between human activity and the detectability of birds is complex and extends beyond a simple masking effect of background noise. Understanding how human activity influences detectability of birds requires consideration of species-specific behavioral responses and how such responses may affect both visual and auditory cues relied on by observers. Detectability reflects both the availability and perceptibility of birds — that is, whether a bird could be detected (i.e., it is visible or vocalizing) and whether it is noted by an observer (Johnson, 2008). Even if a species is known to use a site, it may not always be available to be observed at that location; it may be elsewhere at the time the survey took place, it may be hidden from view, or it may be silent. The positive relationship we observed between human mobility and detection of some species may suggest that these species were more likely to be available where volunteers conducted their surveys as lockdown restrictions eased. Volunteers selected their own monitoring sites, and an overwhelming majority chose to survey birds in their own backyards. Perhaps species that were more readily detected as human mobility increased were more likely to spend time (i.e., be available) in locations volunteers monitored as lockdown restrictions eased, which would suggest that backyards may serve as refugia for birds that are more sensitive to human activity in densely populated areas. On the other hand, synanthropic species that benefit from close association with people may have been more drawn to urban centers as human mobility increased, meaning they were less likely to be observed in backyards; this could explain why detection of American Crows (*Corvus brachyrhynchos*) and Rock Pigeons (*Columba livia*), two urban exploiters, was negatively related to human mobility. However, not all species would or could vary their daily activity in this way; some birds exhibit strong nest site fidelity or maintain small territories during the breeding season, and birds tending to chicks would have been unwilling to travel far from their nests. Birds that did not adjust the spatial component of their daily activity in response to lockdowns may have still altered their behavior in a way that ultimately influenced their detection probability. There are many ways that behavioral responses to human activity could have affected the perceptibility of birds, including shifts in flight speeds, use of vertical space, or changes in vocalization. For example, birds are known to modify their songs to be heard over anthropogenic noise. Perhaps as human activity increased, birds altered their vocalizations to effectively communicate, thereby making themselves more noticeable to human observers, too — especially at times of day when birders could take advantage of such enhanced auditory cues during a lull in anthropogenic noise (i.e., after rush hour). Unfortunately, we cannot parse out the effect of human mobility on the availability and perceptibility of birds, nor attribute the trends we observed to specific components of human activity, such as vehicle traffic. We recommend that future studies explore how species-specific detection probabilities change along the urban-to-rural gradient at various times of day to better understand the relationship between human activity and the detectability of birds.

There is emerging evidence of shifts in avian behavior during COVID-19 lockdowns that may have influenced the probability of detecting birds in the spring of 2020. For example, White-crowned Sparrows sang at lower frequencies and softer volumes during COVID-19 lockdowns in San Francisco, California, USA, where reductions in traffic volume led to a dramatic decline in noise pollution (Derryberry et al., 2020). Both the sparrow's improved song and a drop in background noise contributed to an increase in the distance at which males could be heard singing (Derryberry et al., 2020). Based on these results, we expected that detection of White-crowned Sparrows in the Pacific Northwest would be inversely related to human mobility, which was correlated with traffic volume in our study area. Instead, we found that detection of White-crowned Sparrows was positively related to human mobility. It is possible that White-crowned Sparrows in the Pacific Northwest did not respond to changes in noise pollution in the same way as White-crowned Sparrows in San Francisco; however, we were unable to explicitly examine the effect of noise pollution on detection of birds in this study. Furthermore, the influence of vehicle traffic on noise pollution varies based on road configuration and local vegetation. Therefore, whereas human mobility is a good proxy measurement for traffic volume in our study area, it may not be representative of noise pollution. That said, it is worth noting that volunteers overwhelming indicated that noise pollution either did not change or increased over the course of the data collection campaign, which suggests that noise pollution may have been correlated with human mobility at some monitoring sites. Future research should explore how species-specific responses to lockdowns varied by region and investigate how changes in avian behavior may have ultimately affected the probability of observing birds. Characterizing changes in the detectability of avifauna during the Anthropause is important not only to inform our understanding of how birds respond to sudden shifts in human activity, but also to improve inference when modeling the demographics of bird populations in 2020 (Hochachka et al., 2021).

While research has shown that weather may influence the activity and therefore the detectability of birds (Robbins, 1981a), air pollution may be equally important (Sanderfoot & Gardner, 2021). We found that daily mean air temperature and daily accumulated precipitation were important predictors of detection in 28% and 20% of species, respectively. This is similar to the proportion of species (22%) for which detection was driven by $PM_{2.5}$. We expected that the lockdowns would reduce air pollution in our study area, and improvements in air quality would influence the detectability of birds (Lee et al., 2017); however, $PM_{2.5}$ concentrations increased in both Washington and Oregon in the spring of 2020 as compared to the previous five years (Archer et al., 2020). Regardless, air quality was quite good in our study area during the Anthropause — in our analysis, concentrations of $PM_{2.5}$ ranged between 1 and 11.2 $\mu g/m^3$, with a median value of 3.9 $\mu g/m^3$, which is well below the 24-hour National Ambient Air Quality Standard (NAAQS) of 35 $\mu g/m^3$. This suggests that even at levels deemed safe for human health, air pollution may be driving species-specific behavioral changes in birds that ultimately influence their detectability (e.g., movement, vocalization). Although $PM_{2.5}$ concentrations increased in our study area, concentrations of nitrogen dioxide (NO_2), another urban air pollutant, sharply declined (Archer et al., 2020). Archer et al. (2020) suggested that this may be due to differences in the sources of these two pollutants. Whereas the operation of motor vehicles contributes to both $PM_{2.5}$ and NO_2 pollution, trucks and other diesel vehicles are the primary contributors to $PM_{2.5}$ from traffic. While fewer passenger vehicles were on the road during lockdowns, commercial trucks were still operating as they usually would; consequently, $PM_{2.5}$

was less impacted than NO_2 by the drop in human mobility (Archer et al., 2020). Due to limited availability of NO_2 monitors in our study area, we were unable to consider the effect of this urban air pollutant in our analysis. We recommend that future studies investigate how air and noise pollution from vehicle traffic jointly impact avian behavior and influence the detection and distributions of birds across cities (Leonard et al., 2017). Regional differences in the impacts of COVID-19 lockdowns on local environments provide a unique opportunity to investigate these relationships. Air quality models and data from satellite instruments may be useful in characterizing air pollution across study areas, but given the technical expertise required to use these tools, we recommend that ecologists work in partnership with atmospheric chemists and epidemiologists to build exposure estimates.

By surveying volunteers, we were also able to explore how the availability of seed or suet feeders, hummingbird feeders, and bird baths influenced site use by study species, adding to the limited research to date on how provision of supplementary resources affects the distribution of backyard birds (Cleary et al., 2016; Plummer et al., 2019). We found that bird feeders and bird baths were important predictors of site use for 22% and 13% of backyard birds, respectively. Black-headed Grosbeaks (*Pheucticus melanocephalus*), Dark-eyed Juncos (*Junco hyemalis*), Golden-crowned Sparrows (*Zonotrichia atricapilla*), and Red-breasted Nuthatches were attracted to sites where seed or suet feeders were available, and Anna’s Hummingbirds and Rufous Hummingbirds both showed strong, positive associations with the availability of hummingbird feeders. Some species avoided sites with bird feeders, suggesting that feeders play a role in driving community assemblages in the Pacific Northwest (Plummer et al., 2019). While 6 species were more likely to use sites with bird baths, no species exhibited a statistically significant, negative relationship with bird baths, implying that bird baths only served to attract birds to gardens. Overall, site use by most species was not influenced by availability of bird feeders or bird baths. On the other hand, we found that nearly half of study species exhibited either positive or negative relationships with land cover. This indicates that while provision of supplementary resources did increase the probability that some species used a site, land use is a stronger driver of species distributions in urban areas. Our findings support the push by many conservation non-profits to maintain large parks within cities and plant native vegetation in gardens to support the continued success of backyard birds.

We were most interested in how land cover drove site use by urban exploiters during the Anthropause. Predictably, we found that European Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*), and Glaucous-winged Gulls (*Larus glaucescens*) were positively associated with highly developed areas. European Starlings and House Sparrows are well-established synanthropes, and Glaucous-winged Gulls are commonly observed scavenging at landfills or in parking lots. On the other hand, American Crows, also an urban exploiter, were negatively associated with highly developed areas. Like Glaucous-winged Gulls, American Crows are omnivorous ground foragers, known to search for food in trashcans and garbage dumps in urban areas. We hypothesize that unlike gulls, a species that is restricted to the coastline, crows may have moved away from urban centers during COVID-19 lockdowns due to limited foraging opportunities, perhaps because less trash was generated by businesses, bars, and restaurants. Canopy cover had a statistically significant effect on site use for 20% of study species. As we expected, both bark gleaners (Downy Woodpecker [*Dryobates pubescens*] and Red-breasted Nuthatch) exhibited positive relationships with canopy cover and several urban exploiters, including European Starling and House Sparrow, were less likely to use sites with greater canopy cover. Still, neither land use nor canopy cover influenced site use by most species (52%). This suggests that either the species included in our analysis are well-adapted to urban settings and can make use of a wide variety of habitats within cities, or that variables other than percent impervious surface and canopy cover may be more meaningful in describing how urbanization drives bird distributions.

Our results also show that the probability of detecting birds was impacted by seasonality and time of day. The probability of detecting 78% of study species was influenced by day of year and/or day of year squared, suggesting that there is temporal variation in the availability and/or perceptibility of backyard birds during the breeding season in the Pacific Northwest and that this variation may be linear and/or quadratic. The effect of seasonality on detection was particularly strong for Golden-crowned Sparrows and Ruby-crowned Kinglets (*Regulus calendula*), species that spend the breeding season further north or at high elevations; both Golden-crowned Sparrows and Ruby-crowned Kinglets were much less likely to be observed by volunteers later in the spring. Time of day was also an important predictor of detection across taxa — time of day and/or time of day squared drove detection of 83% of study species. Birds exhibit species-specific patterns in daily activity that influence the probability of detecting them, with many species most active at or shortly after sunrise (Robbins, 1981b). While our results do suggest that many backyard birds were more readily observed earlier in the day, our results also indicate that several species were more likely to be observed later in the day as well (Table 5.1).

Finally, our study illustrates the value of volunteer-collected data and the potential for community science to rapidly expand our understanding of what drives detection and distributions of birds in urban areas. Volunteers helped us monitor birds at much larger spatial and temporal extents than we could have surveyed on our own, and because so many people participated, we were able to consider the impact of fine scale shifts in land use and environmental conditions on birds within urban areas. In addition, unlike other analyses of eBird data filtered post hoc, we were able to collect data according to a standardized protocol, which strengthens our inference by minimizing bias between surveys. We also regularly communicated with volunteers, answering questions about our survey protocol and connecting less experienced birders with birding mentors. This allowed us to minimize errors in data collection and reduce species misidentifications. While we did encourage beginner birders to participate in this project — 22% of questionnaire respondents indicated that they were beginner or novice birders — we feel confident that the controls we had in place ensured collection of high-quality data. In a post-hoc analysis, we explored the effect of expertise on detection of study species. We found that while volunteers who described themselves as advanced birders were more likely to detect some study species, the effect of birding ability on detection varied by species and within levels of expertise — in fact, beginner birders were more likely than advanced birders to detect some species. We have no reason to believe that there is any systematic bias in the spatial and temporal sampling by novice and expert birders. In addition, questionnaire respondents overwhelming indicated that they were confident or highly confident that they followed our survey protocol. Furthermore, because we were in direct contact with volunteers, we were able to collect additional information about their monitoring sites, adding richness to our dataset and allowing us to answer questions that would have otherwise been impossible to explore. We believe our community science project is an excellent example of the power of volunteer-collected data, and we hope that more ecologists will consider using community science to answer challenging ecological questions, particularly when it is necessary to collect data immediately and at a large spatial extent. Our project suggests that leveraging pre-existing community science infrastructure (e.g., eBird) allows for rapid project development. Furthermore, volunteers may be more interested in participating in community science projects in times of crisis — 85% of volunteers who responded to our online questionnaire indicated that the pandemic played a role in prompting them to sign up.

5.5 CONCLUSION

Urban populations are on the rise around the world; as such, it is imperative that we investigate species-specific responses to urbanization to inform conservation strategies for birds that live along the urban-to-rural gradient. This requires disentangling complex relationships between land use, weather, air pollution, and human mobility and the presence and detection of birds. Our study demonstrates that backyard birds vary widely in their responses to abiotic and biotic components of urban habitat and suggests that future research should focus on teasing out how human mobility and air pollution influences the presence, availability, and perceptibility of birds in cities. We recommend greater use of community science by ecologists and encourage researchers to consider the value of engaging directly with volunteers.

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APPENDIX A

This appendix includes additional information about the keyword search executed as part of the literature review presented in chapter 2. We refined results from our initial keyword search in Web of Science to include only articles from categories deemed relevant to our literature review. We considered the top 100 Web of Science categories for each keyword search. Articles from the following categories were included from each keyword search.

<u>fire* AND smoke*</u>

Environmental Sciences, Public Environmental Occupational Health, Forestry, Plant Sciences, Ecology, Geosciences Multidisciplinary, Toxicology, Medicine General Internal, Multidisciplinary Sciences, Remote Sensing, Respiratory System, Environmental Studies, Oceanography, Water Resources, Biodiversity Conservation, Cardiac Cardiovascular Systems, Mathematics Interdisciplinary Applications, Biochemistry Molecular Biology, Computer Science Interdisciplinary Applications, Agriculture Multidisciplinary, Oncology, Biotechnology Applied Microbiology, Veterinary Sciences, Agronomy, Physiology, Biology, Infectious Diseases, Allergy, Genetics Heredity, Immunology

<u>wildfire* AND smoke*</u>

Environmental Sciences, Public Environmental Occupational Health, Forestry, Geosciences Multidisciplinary, Remote Sensing, Toxicology, Ecology, Multidisciplinary Sciences, Environmental Studies, Respiratory System, Plant Sciences, Water Resources, Oceanography, Medicine General Internal, Biodiversity Conservation, Biochemistry Molecular Biology, Geography, Agriculture Multidisciplinary, Allergy, Biology, Cardiac Cardiovascular Systems, Immunology, Marine Freshwater Biology, Agronomy, Cell Biology, Communication, Computer Science Interdisciplinary Applications, Development Studies, Genetics Heredity, Mathematics Interdisciplinary Applications, Physiology, Statistics Probability, Area Studies, Behavioral Sciences, Biotechnology Applied Microbiology, Developmental Biology, Entomology, Evolutionary Biology, Horticulture, Limnology, Mathematical Computational Biology

APPENDIX B

This appendix includes additional information about how we processed air quality data used in the analysis presented in chapter 3.

If more than one daily $PM_{2.5}$ concentration measurement was available for an air quality monitoring site on a given day, we used observations with an AQS parameter code of 88101. This parameter code refers to data collected by instruments that can be used to assess compliance with the National Ambient Air Quality Standards (NAAQS). If multiple daily $PM_{2.5}$ concentration measurements were still available for a single air quality monitoring site after selecting observations with a parameter code of 88101, we used the observation associated with the smallest parameter occurrence code (POC). POCs are used to differentiate multiple sensors at a monitoring site that all measure the same parameter; using the smallest code ensured that we used measurements collected by Federal Reference Method (FRM) samplers when available.

APPENDIX C

This appendix includes complete model results for the analysis presented in chapter 3.

Table A.1: Complete model results for all 71 study species. The table shows the estimated coefficients and 95% confidence intervals on the logit scale for the fixed effects of year, land cover class, day of year, day of year squared, time observations started, duration of survey, distance traveled, daily mean air temperature, daily accumulated precipitation, and daily mean concentration of $PM_{2.5}$ for each of the 71 study species. We also included the p-value on the fixed effect of $PM_{2.5}$. The estimate and its p-value are in bold font if the effect was statistically significant ($p < 0.05$). Conditional R^2 and AIC values are also reported for each model. An asterisk next to the AIC value indicates that including the effect of $PM_{2.5}$ improved model fit as compared to the null model. Two asterisks indicate that the delta AIC value was greater than 2. Model results are reported by species and ordered based on the number of detections of that species in our final dataset.

	American Robin	**Black-capped Chickadee**	**American Crow**	**Song Sparrow**	**Northern Flicker**	**Great Blue Heron**	**Barn Swallow**	**Mallard**
No. of detections	25,527	25,437	24,974	24,639	19,947	19,736	18,924	18,868
Intercept	-1.063 (-1.139, -0.986)	-0.611 (-0.696, -0.527)	-0.937 (-1.029, -0.845)	-1.456 (-1.54, -1.372)	-1.391 (-1.471, -1.312)	-1.076 (-1.152, -1)	-0.689 (-0.773, -0.605)	-1.25 (-1.333, -1.168)
2016	0.012 (-0.058, 0.081)	-0.074 (-0.147, -0.002)	0.13 (0.054, 0.205)	0.075 (0.004, 0.147)	0.107 (0.035, 0.178)	-0.059 (-0.129, 0.012)	-0.168 (-0.242, -0.093)	0 (-0.072, 0.072)
2017	-0.116 (-0.183, -0.048)	-0.148 (-0.219, -0.078)	0.136 (0.063, 0.209)	-0.045 (-0.115, 0.024)	-0.059 (-0.129, 0.011)	-0.134 (-0.203, -0.066)	-0.314 (-0.386, -0.242)	-0.122 (-0.192, -0.052)
2018	0.099 (0.033, 0.165)	-0.035 (-0.104, 0.034)	0.07 (-0.002, 0.142)	0 (-0.068, 0.068)	0.015 (-0.053, 0.084)	-0.214 (-0.281, -0.147)	-0.359 (-0.431, -0.288)	-0.224 (-0.293, -0.155)
Barren	-0.62 (-0.704, -0.536)	-0.683 (-0.767, -0.599)	-0.092 (-0.176, -0.008)	-0.049 (-0.129, 0.031)	-0.729 (-0.819, -0.639)	1.206 (1.13, 1.282)	0.815 (0.735, 0.896)	0.119 (0.038, 0.2)
Cultivated	0.313 (0.227, 0.4)	-0.079 (-0.169, 0.012)	-0.329 (-0.421, -0.238)	0.037 (-0.054, 0.128)	0.135 (0.045, 0.225)	-0.018 (-0.111, 0.075)	0.658 (0.567, 0.749)	-0.049 (-0.142, 0.043)
Forest	0.392 (0.324, 0.461)	-0.104 (-0.174, -0.034)	-0.847 (-0.924, -0.77)	0.228 (0.158, 0.299)	0.196 (0.125, 0.267)	-0.694 (-0.779, -0.61)	-1.06 (-1.15, -0.969)	-1.086 (-1.179, -0.994)
Herbaceous	0.03 (-0.075, 0.134)	-0.144 (-0.257, -0.031)	-0.26 (-0.373, -0.147)	0.39 (0.283, 0.497)	0.034 (-0.073, 0.141)	0.161 (0.056, 0.266)	0.506 (0.396, 0.616)	-0.316 (-0.427, -0.205)
Water	-0.978 (-1.051, -0.905)	-1.201 (-1.277, -1.126)	-0.368 (-0.438, -0.297)	-0.527 (-0.598, -0.456)	-0.862 (-0.938, -0.786)	0.905 (0.842, 0.969)	0.441 (0.372, 0.51)	0.576 (0.51, 0.641)
Shrubland	-0.118 (-0.215, -0.021)	-0.968 (-1.078, -0.857)	-1.399 (-1.52, -1.278)	-0.534 (-0.642, -0.427)	-0.089 (-0.189, 0.01)	-0.23 (-0.336, -0.124)	-0.238 (-0.349, -0.128)	-0.416 (-0.523, -0.31)
Wetlands	0.448 (0.383, 0.514)	0.471 (0.404, 0.538)	-0.232 (-0.301, -0.162)	1.07 (1.001, 1.138)	0.162 (0.095, 0.229)	1.463 (1.398, 1.529)	1.144 (1.075, 1.213)	1.44 (1.373, 1.506)
Day	-0.482 (-0.505, -0.459)	0.108 (0.085, 0.132)	-0.007 (-0.031, 0.018)	-0.001 (-0.024, 0.022)	0.331 (0.308, 0.354)	0.175 (0.151, 0.199)	-0.784 (-0.812, -0.755)	0.254 (0.23, 0.279)
Day^2	0.441 (0.417, 0.465)	0.049 (0.025, 0.074)	0.125 (0.1, 0.151)	0.431 (0.407, 0.455)	0.306 (0.282, 0.331)	-0.047 (-0.072, -0.023)	-0.596 (-0.624, -0.567)	-0.011 (-0.037, 0.014)
Time	-0.296 (-0.318, -0.275)	-0.371 (-0.393, -0.348)	-0.281 (-0.303, -0.258)	-0.384 (-0.406, -0.362)	-0.368 (-0.391, -0.345)	-0.118 (-0.14, -0.096)	-0.083 (-0.106, -0.06)	-0.068 (-0.09, -0.046)
Duration	0.593 (0.562, 0.623)	0.552 (0.522, 0.583)	0.274 (0.246, 0.301)	0.574 (0.543, 0.605)	0.56 (0.531, 0.588)	0.352 (0.326, 0.377)	0.365 (0.337, 0.393)	0.264 (0.238, 0.289)
Distance	0.157 (0.134, 0.18)	0.022 (-0.002, 0.045)	-0.027 (-0.051, -0.003)	0.062 (0.038, 0.085)	0.124 (0.102, 0.146)	0.126 (0.105, 0.148)	0.142 (0.119, 0.165)	0.088 (0.065, 0.11)
Temperature	-0.05 (-0.077, -0.024)	0.094 (0.067, 0.122)	0.069 (0.041, 0.097)	-0.001 (-0.029, 0.026)	0.037 (0.01, 0.064)	0.105 (0.077, 0.132)	-0.091 (-0.119, -0.063)	0.243 (0.216, 0.271)
Precipitation	-0.037 (-0.059, -0.016)	0 (-0.02, 0.021)	0.002 (-0.02, 0.024)	0.018 (-0.002, 0.039)	-0.023 (-0.044, -0.002)	0.025 (0.004, 0.045)	0.059 (0.037, 0.082)	0.049 (0.028, 0.069)
$PM_{2.5}$	0.016 (-0.005, 0.037)	0.005 (-0.016, 0.026)	0.015 (-0.007, 0.038)	-0.003 (-0.026, 0.02)	0.011 (-0.01, 0.032)	**-0.034 (-0.058, -0.011)**	0.014 (-0.009, 0.036)	-0.013 (-0.035, 0.008)
p-value ($PM_{2.5}$)	0.13	0.65	0.19	0.81	0.30	**4.1×10^{-3}**	0.23	0.23
Conditional R^2	0.39	0.42	0.44	0.42	0.34	0.31	0.44	0.36
AIC	69021.51*	67419.96	64395.08	67230.97	65294.61	64785.32**	60343.35	63405.87

	American Goldfinch	**Spotted Towhee**	**European Starling**	**House Finch**	**Cedar Waxwing**	**Steller's Jay**	**Anna's Hummingbird**
No. of detections	18,789	17,791	17,054	16,118	14,147	14,126	13,988
Intercept	-1.213 (-1.298, -1.127)	-1.955 (-2.047, -1.863)	-1.416 (-1.498, -1.334)	-1.782 (-1.878, -1.686)	-1.447 (-1.535, -1.359)	-1.581 (-1.677, -1.485)	-1.971 (-2.079, -1.864)
2016	-0.033 (-0.106, 0.04)	0.088 (0.009, 0.166)	-0.082 (-0.155, -0.01)	0.088 (0.011, 0.166)	-0.044 (-0.123, 0.035)	-0.119 (-0.202, -0.035)	0.191 (0.104, 0.278)
2017	-0.201 (-0.272, -0.129)	0.148 (0.072, 0.223)	-0.073 (-0.142, -0.003)	-0.03 (-0.105, 0.045)	-0.12 (-0.197, -0.043)	-0.048 (-0.129, 0.032)	0.16 (0.076, 0.245)
2018	-0.111 (-0.181, -0.041)	0.211 (0.136, 0.285)	-0.214 (-0.283, -0.145)	0.137 (0.064, 0.211)	-0.048 (-0.123, 0.027)	-0.241 (-0.32, -0.161)	0.491 (0.408, 0.573)
Barren	-0.491 (-0.58, -0.401)	-0.665 (-0.759, -0.571)	0.096 (0.014, 0.177)	-0.425 (-0.517, -0.334)	-0.234 (-0.33, -0.139)	-1.115 (-1.224, -1.006)	-0.874 (-0.977, -0.772)
Cultivated	0.423 (0.335, 0.511)	-0.115 (-0.216, -0.014)	0.497 (0.411, 0.584)	0.008 (-0.086, 0.102)	0.327 (0.234, 0.421)	-0.232 (-0.341, -0.124)	-0.32 (-0.433, -0.206)
Forest	-0.739 (-0.82, -0.659)	0.602 (0.531, 0.674)	-1.713 (-1.819, -1.608)	-1.007 (-1.099, -0.915)	-0.343 (-0.426, -0.259)	0.627 (0.551, 0.703)	-0.392 (-0.475, -0.308)
Herbaceous	0.27 (0.166, 0.375)	0.351 (0.242, 0.461)	-0.384 (-0.494, -0.273)	-0.017 (-0.128, 0.094)	0.564 (0.453, 0.675)	-0.071 (-0.195, 0.052)	0.003 (-0.119, 0.125)
Water	-0.835 (-0.914, -0.755)	-1.356 (-1.448, -1.265)	-0.165 (-0.234, -0.096)	-0.9 (-0.982, -0.818)	-0.608 (-0.693, -0.522)	-1.294 (-1.392, -1.197)	-1.533 (-1.637, -1.428)
Shrubland	-0.722 (-0.831, -0.612)	-0.319 (-0.433, -0.205)	-0.8 (-0.909, -0.69)	-0.726 (-0.841, -0.612)	-0.426 (-0.541, -0.311)	-0.395 (-0.525, -0.264)	-1.226 (-1.386, -1.066)
Wetlands	0.595 (0.528, 0.662)	0.062 (-0.009, 0.133)	0.447 (0.381, 0.513)	-0.233 (-0.307, -0.16)	0.834 (0.765, 0.903)	-0.637 (-0.718, -0.555)	-0.453 (-0.533, -0.372)
Day	-0.351 (-0.376, -0.326)	-0.101 (-0.125, -0.076)	0.003 (-0.021, 0.027)	-0.007 (-0.033, 0.018)	-0.47 (-0.497, -0.442)	0.446 (0.418, 0.474)	0.278 (0.25, 0.307)
Day^2	-0.047 (-0.072, -0.021)	0.359 (0.333, 0.385)	0.176 (0.151, 0.201)	0.084 (0.058, 0.111)	-0.187 (-0.215, -0.159)	0.011 (-0.018, 0.04)	0.028 (-0.001, 0.057)
Time	-0.341 (-0.364, -0.318)	-0.425 (-0.45, -0.4)	-0.308 (-0.331, -0.285)	-0.357 (-0.382, -0.333)	-0.199 (-0.223, -0.174)	-0.498 (-0.526, -0.47)	-0.435 (-0.463, -0.408)
Duration	0.532 (0.503, 0.561)	0.5 (0.47, 0.53)	0.25 (0.224, 0.276)	0.424 (0.395, 0.453)	0.494 (0.465, 0.522)	0.468 (0.437, 0.499)	0.531 (0.497, 0.565)
Distance	-0.033 (-0.057, -0.009)	0.083 (0.058, 0.107)	0.119 (0.097, 0.141)	-0.11 (-0.136, -0.084)	0.16 (0.136, 0.183)	0.048 (0.021, 0.075)	-0.227 (-0.261, -0.192)
Temperature	-0.013 (-0.041, 0.015)	-0.029 (-0.059, 0.001)	0.06 (0.032, 0.087)	0.156 (0.127, 0.185)	-0.146 (-0.176, -0.116)	-0.135 (-0.168, -0.101)	0.085 (0.05, 0.12)
Precipitation	-0.059 (-0.084, -0.035)	-0.013 (-0.036, 0.01)	-0.002 (-0.024, 0.02)	-0.022 (-0.046, 0.002)	-0.033 (-0.059, -0.008)	-0.026 (-0.049, -0.004)	-0.002 (-0.026, 0.022)
$PM_{2.5}$	0.012 (-0.01, 0.034)	**0.04 (0.016, 0.064)**	0.003 (-0.019, 0.025)	-0.011 (-0.033, 0.012)	**0.039 (0.016, 0.062)**	0.021 (-0.005, 0.048)	-0.012 (-0.04, 0.015)
p-value ($PM_{2.5}$)	0.28	**9.3 x 10^{-4}**	0.80	0.35	**1.0 x 10^{-3}**	0.11	.38
Conditional R^2	0.39	0.42	0.33	0.38	0.37	0.44	0.47
AIC	62210.58	59388.31**	62186.19	58118.40	55611.59**	51749.02*	51358.27

	Canada Goose	**Dark-eyed Junco**	**White-crowned Sparrow**	**Glaucous-winged Gull**	**Belted Kingfisher**	**Red-breasted Nuthatch**	**Bewick's Wren**
No. of detections	13,838	13,798	13,769	13,728	13,000	12,955	12,576
Intercept	-1.67 (-1.752, -1.588)	-2.202 (-2.299, -2.105)	-2.019 (-2.108, -1.93)	-2.02 (-2.129, -1.911)	-1.43 (-1.513, -1.347)	-1.669 (-1.768, -1.569)	-2.494 (-2.606, -2.381)
2016	0.014 (-0.062, 0.089)	-0.033 (-0.118, 0.053)	-0.007 (-0.084, 0.071)	-0.036 (-0.121, 0.049)	-0.117 (-0.193, -0.042)	-0.375 (-0.461, -0.29)	0.236 (0.148, 0.324)
2017	0.044 (-0.028, 0.116)	0.29 (0.208, 0.371)	0.06 (-0.014, 0.135)	0.093 (0.011, 0.175)	-0.285 (-0.359, -0.211)	-0.002 (-0.083, 0.078)	0.045 (-0.041, 0.13)
2018	-0.072 (-0.143, 0)	0.095 (0.014, 0.176)	0.049 (-0.025, 0.122)	-0.274 (-0.357, -0.192)	-0.342 (-0.415, -0.27)	-0.102 (-0.181, -0.023)	0.285 (0.202, 0.369)
Barren	0.505 (0.423, 0.587)	-1.085 (-1.197, -0.973)	-0.002 (-0.088, 0.084)	1.011 (0.926, 1.097)	0.495 (0.411, 0.579)	-1.246 (-1.368, -1.125)	-0.452 (-0.555, -0.349)
Cultivated	0.418 (0.325, 0.51)	-0.311 (-0.423, -0.199)	0.131 (0.037, 0.226)	-0.657 (-0.784, -0.529)	-0.084 (-0.191, 0.024)	-0.539 (-0.656, -0.421)	-0.506 (-0.631, -0.381)
Forest	-1.092 (-1.197, -0.987)	0.865 (0.792, 0.938)	-0.565 (-0.651, -0.479)	-0.482 (-0.576, -0.388)	-0.315 (-0.404, -0.225)	1.116 (1.042, 1.19)	-0.111 (-0.199, -0.023)
Herbaceous	-0.676 (-0.808, -0.544)	0.317 (0.201, 0.433)	0.651 (0.546, 0.755)	0.46 (0.341, 0.579)	-0.325 (-0.454, -0.196)	0.182 (0.065, 0.3)	0.087 (-0.038, 0.212)
Water	0.67 (0.602, 0.737)	-1.29 (-1.391, -1.19)	-0.546 (-0.625, -0.466)	1.257 (1.184, 1.329)	0.697 (0.627, 0.767)	-1.189 (-1.29, -1.089)	-1.009 (-1.108, -0.909)
Shrubland	-0.478 (-0.596, -0.359)	0.357 (0.244, 0.469)	-0.323 (-0.437, -0.21)	-1.362 (-1.552, -1.171)	-0.427 (-0.554, -0.299)	-0.04 (-0.154, 0.073)	-0.743 (-0.888, -0.599)
Wetlands	0.942 (0.876, 1.009)	-0.925 (-1.013, -0.838)	-0.009 (-0.081, 0.063)	0.152 (0.072, 0.232)	1.076 (1.007, 1.144)	-0.919 (-1.01, -0.828)	0.332 (0.253, 0.411)
Day	0.161 (0.136, 0.187)	-0.022 (-0.048, 0.004)	-0.041 (-0.065, -0.016)	0.118 (0.089, 0.147)	0.225 (0.198, 0.251)	0.109 (0.081, 0.137)	0.214 (0.185, 0.244)
Day^2	-0.059 (-0.085, -0.032)	0.428 (0.4, 0.455)	0.27 (0.244, 0.296)	-0.056 (-0.086, -0.026)	-0.174 (-0.201, -0.146)	-0.118 (-0.147, -0.089)	0.086 (0.056, 0.116)
Time	-0.102 (-0.126, -0.078)	-0.299 (-0.325, -0.273)	-0.229 (-0.253, -0.204)	-0.043 (-0.07, -0.017)	-0.184 (-0.209, -0.158)	-0.442 (-0.47, -0.414)	-0.54 (-0.57, -0.51)
Duration	0.255 (0.23, 0.28)	0.472 (0.443, 0.501)	0.353 (0.327, 0.38)	0.259 (0.228, 0.29)	0.412 (0.384, 0.439)	0.436 (0.407, 0.466)	0.462 (0.43, 0.493)
Distance	0.085 (0.062, 0.107)	0.083 (0.057, 0.108)	0.063 (0.04, 0.087)	0.114 (0.086, 0.141)	0.079 (0.055, 0.102)	0.034 (0.008, 0.061)	0.046 (0.017, 0.075)
Temperature	0.155 (0.127, 0.184)	-0.162 (-0.195, -0.13)	-0.239 (-0.269, -0.208)	-0.034 (-0.069, 0.001)	0.024 (-0.007, 0.055)	-0.102 (-0.134, -0.069)	0.214 (0.179, 0.249)
Precipitation	-0.006 (-0.028, 0.017)	-0.043 (-0.068, -0.017)	-0.044 (-0.068, -0.021)	0.062 (0.039, 0.085)	0.001 (-0.022, 0.023)	-0.079 (-0.106, -0.051)	-0.005 (-0.031, 0.022)
$PM_{2.5}$	**-0.048 (-0.072, -0.024)**	0.019 (-0.008, 0.046)	0.01 (-0.016, 0.036)	-0.028 (-0.059, 0.004)	-0.011 (-0.036, 0.015)	**0.052 (0.029, 0.075)**	-0.015 (-0.043, 0.014)
p-value ($PM_{2.5}$)	**1.0 x 10^{-4}**	0.17	0.45	0.09	0.42	**1.1 x 10^{-5}**	0.31
Conditional R^2	0.27	0.40	0.30	0.49	0.29	0.43	0.47
AIC	57555.22**	52593.80	57434.20	51121.37*	55148.45	51128.99**	47346.07

	Killdeer	**Chestnut-backed Chickadee**	**California Gull**	**Osprey**	**Rock Pigeon**	**Red-winged Blackbird**	**Double-crested Cormorant**
No. of detections	12,447	11,582	10,770	10,259	9,758	9,665	9,145
Intercept	-2.106 (-2.201, -2.011)	-1.962 (-2.069, -1.855)	-2.429 (-2.544, -2.314)	-1.993 (-2.092, -1.893)	-1.973 (-2.075, -1.87)	-2.788 (-2.893, -2.683)	-2.702 (-2.805, -2.599)
2016	0.024 (-0.056, 0.104)	-0.083 (-0.172, 0.006)	-0.087 (-0.177, 0.003)	-0.001 (-0.09, 0.087)	-0.007 (-0.097, 0.082)	-0.015 (-0.106, 0.075)	-0.078 (-0.167, 0.011)
2017	-0.094 (-0.171, -0.016)	-0.137 (-0.224, -0.05)	0.11 (0.024, 0.197)	0.019 (-0.066, 0.104)	0.117 (0.031, 0.202)	-0.174 (-0.262, -0.087)	-0.142 (-0.229, -0.056)
2018	-0.033 (-0.11, 0.043)	0.001 (-0.083, 0.086)	-0.004 (-0.09, 0.082)	0.068 (-0.016, 0.152)	-0.125 (-0.211, -0.039)	-0.077 (-0.163, 0.009)	-0.093 (-0.179, -0.008)
Barren	0.828 (0.744, 0.913)	-0.629 (-0.736, -0.522)	1.434 (1.345, 1.523)	0.68 (0.587, 0.772)	0.21 (0.118, 0.301)	-0.384 (-0.512, -0.257)	1.567 (1.476, 1.658)
Cultivated	0.28 (0.181, 0.38)	-0.659 (-0.79, -0.529)	-0.162 (-0.291, -0.033)	0.026 (-0.093, 0.144)	-0.638 (-0.767, -0.51)	0.284 (0.177, 0.39)	-0.4 (-0.548, -0.252)
Forest	-1.726 (-1.868, -1.585)	1.132 (1.054, 1.21)	-0.436 (-0.547, -0.325)	-0.703 (-0.814, -0.592)	-1.812 (-1.956, -1.668)	-1.312 (-1.449, -1.175)	0.118 (0.012, 0.223)
Herbaceous	0.135 (0.015, 0.255)	0.568 (0.446, 0.69)	0.917 (0.796, 1.038)	0.32 (0.195, 0.445)	-0.225 (-0.353, -0.097)	-0.489 (-0.646, -0.331)	0.669 (0.539, 0.798)
Water	0.668 (0.596, 0.74)	-1.097 (-1.2, -0.993)	1.365 (1.288, 1.442)	0.477 (0.397, 0.558)	0.378 (0.303, 0.453)	0.303 (0.217, 0.388)	1.501 (1.422, 1.579)
Shrubland	-0.006 (-0.121, 0.109)	-0.534 (-0.681, -0.388)	-0.284 (-0.434, -0.134)	-0.298 (-0.435, -0.16)	-1.303 (-1.479, -1.127)	-0.148 (-0.271, -0.026)	0.122 (-0.019, 0.262)
Wetlands	1.049 (0.979, 1.119)	-0.653 (-0.743, -0.563)	0.267 (0.179, 0.354)	0.76 (0.683, 0.836)	-0.33 (-0.416, -0.243)	1.609 (1.534, 1.684)	0.811 (0.726, 0.896)
Day	0.112 (0.085, 0.14)	0 (-0.03, 0.029)	0.345 (0.313, 0.378)	-0.205 (-0.236, -0.174)	0.137 (0.107, 0.167)	-0.093 (-0.122, -0.065)	0.52 (0.488, 0.552)
Day^2	-0.056 (-0.084, -0.027)	-0.052 (-0.083, -0.022)	-0.321 (-0.354, -0.287)	-0.312 (-0.344, -0.28)	-0.077 (-0.109, -0.046)	0.413 (0.383, 0.444)	0.057 (0.025, 0.09)
Time	-0.093 (-0.118, -0.068)	-0.288 (-0.316, -0.259)	-0.045 (-0.074, -0.017)	-0.114 (-0.142, -0.087)	-0.228 (-0.256, -0.2)	-0.215 (-0.244, -0.187)	-0.045 (-0.075, -0.015)
Duration	0.261 (0.234, 0.288)	0.514 (0.482, 0.546)	0.249 (0.219, 0.28)	0.363 (0.335, 0.391)	0.138 (0.108, 0.168)	0.299 (0.271, 0.327)	0.224 (0.196, 0.252)
Distance	-0.026 (-0.051, -0.001)	0.02 (-0.009, 0.049)	0.129 (0.102, 0.157)	0.122 (0.096, 0.147)	0.153 (0.128, 0.179)	0.115 (0.09, 0.14)	0.163 (0.138, 0.188)
Temperature	0.256 (0.226, 0.287)	-0.116 (-0.153, -0.08)	-0.035 (-0.071, 0)	0.148 (0.115, 0.182)	0.123 (0.089, 0.157)	0.142 (0.108, 0.175)	-0.01 (-0.046, 0.026)
Precipitation	-0.016 (-0.041, 0.01)	0.003 (-0.022, 0.028)	0.014 (-0.012, 0.04)	0.019 (-0.008, 0.047)	-0.006 (-0.033, 0.021)	-0.007 (-0.037, 0.022)	0.023 (-0.001, 0.047)
PM$_{2.5}$	**-0.036 (-0.06, -0.012)**	0.007 (-0.024, 0.038)	**-0.066 (-0.098, -0.035)**	**-0.039 (-0.066, -0.013)**	-0.016 (-0.042, 0.01)	0.003 (-0.024, 0.031)	**-0.051 (-0.085, -0.017)**
p-value (PM$_{2.5}$)	**3.6×10^{-3}**	0.65	**3.2×10^{-5}**	**3.4×10^{-3}**	0.22	0.81	**0.003**
Conditional R^2	0.37	0.46	0.48	0.35	0.37	0.38	0.36
AIC	52538.39**	47026.73	44304.27**	46985.35**	45869.45	43337.52	42861.1**

	Caspian Tern	**Eurasian Collared-Dove**	**Violet-green Swallow**	**Common Raven**	**House Sparrow**	**Savannah Sparrow**	**Bald Eagle**
No. of detections	9,003	8,820	8,676	8,557	8,498	8,399	8,309
Intercept	-2.689 (-2.803, -2.575)	-2.801 (-2.93, -2.672)	-2.631 (-2.742, -2.519)	-2.894 (-3.005, -2.784)	-2.535 (-2.654, -2.416)	-2.834 (-2.949, -2.719)	-2.666 (-2.773, -2.559)
2016	-0.168 (-0.265, -0.071)	0.217 (0.12, 0.313)	-0.074 (-0.167, 0.02)	0.169 (0.075, 0.263)	0.088 (-0.01, 0.186)	-0.052 (-0.145, 0.04)	0.007 (-0.089, 0.102)
2017	0.232 (0.141, 0.324)	0.205 (0.111, 0.299)	-0.191 (-0.283, -0.1)	0.136 (0.044, 0.227)	0.078 (-0.016, 0.171)	-0.222 (-0.313, -0.131)	0.144 (0.052, 0.237)
2018	0.421 (0.331, 0.511)	0.153 (0.059, 0.246)	-0.178 (-0.267, -0.089)	0.177 (0.088, 0.267)	0.018 (-0.075, 0.11)	-0.284 (-0.373, -0.194)	0.124 (0.033, 0.214)
Barren	1.751 (1.662, 1.84)	-0.342 (-0.463, -0.221)	-0.403 (-0.522, -0.283)	-0.021 (-0.142, 0.1)	-0.19 (-0.299, -0.082)	0.527 (0.428, 0.626)	0.684 (0.583, 0.785)
Cultivated	-0.839 (-1.01, -0.669)	0.571 (0.471, 0.671)	0.427 (0.316, 0.538)	0.866 (0.762, 0.969)	-0.102 (-0.209, 0.005)	0.625 (0.514, 0.735)	0.15 (0.021, 0.278)
Forest	-0.696 (-0.826, -0.567)	-1.371 (-1.509, -1.233)	-0.563 (-0.669, -0.457)	0.838 (0.748, 0.928)	-1.6 (-1.742, -1.459)	-1.855 (-2.023, -1.688)	-0.038 (-0.141, 0.065)
Herbaceous	1.227 (1.105, 1.35)	-0.554 (-0.711, -0.397)	-0.115 (-0.261, 0.032)	0.507 (0.376, 0.638)	-1.195 (-1.376, -1.014)	0.84 (0.717, 0.963)	0.577 (0.444, 0.711)
Water	1.297 (1.216, 1.378)	-0.331 (-0.426, -0.237)	-0.339 (-0.438, -0.241)	-0.176 (-0.276, -0.075)	-0.466 (-0.558, -0.374)	-0.08 (-0.175, 0.016)	0.443 (0.351, 0.534)
Shrubland	-0.893 (-1.105, -0.682)	-0.444 (-0.573, -0.314)	-0.108 (-0.241, 0.024)	1.167 (1.055, 1.278)	-0.744 (-0.884, -0.604)	-0.756 (-0.919, -0.593)	-0.293 (-0.45, -0.137)
Wetlands	0.696 (0.611, 0.782)	0.131 (0.043, 0.218)	0.412 (0.328, 0.497)	0.341 (0.251, 0.431)	-0.935 (-1.04, -0.83)	0.958 (0.879, 1.038)	1.238 (1.158, 1.319)
Day	-0.047 (-0.081, -0.012)	-0.098 (-0.131, -0.065)	-0.951 (-0.986, -0.915)	0.12 (0.09, 0.151)	-0.242 (-0.274, -0.209)	0.218 (0.188, 0.249)	-0.52 (-0.552, -0.487)
Day^2	-0.362 (-0.398, -0.327)	-0.119 (-0.153, -0.085)	0.117 (0.083, 0.151)	-0.029 (-0.061, 0.004)	0.119 (0.086, 0.153)	0.26 (0.227, 0.292)	-0.033 (-0.066, 0)
Time	0.026 (-0.004, 0.056)	-0.225 (-0.254, -0.195)	-0.205 (-0.234, -0.175)	-0.29 (-0.32, -0.259)	-0.211 (-0.24, -0.181)	-0.198 (-0.23, -0.167)	-0.17 (-0.2, -0.14)
Duration	0.292 (0.261, 0.323)	0.204 (0.172, 0.235)	0.32 (0.291, 0.35)	0.302 (0.275, 0.33)	0.123 (0.091, 0.154)	0.379 (0.348, 0.409)	0.407 (0.378, 0.437)
Distance	0.052 (0.022, 0.082)	0.052 (0.025, 0.079)	0.159 (0.132, 0.186)	0.273 (0.249, 0.298)	-0.06 (-0.09, -0.03)	0.254 (0.228, 0.28)	0.154 (0.128, 0.18)
Temperature	0.093 (0.055, 0.131)	0.034 (-0.001, 0.068)	-0.381 (-0.418, -0.344)	-0.23 (-0.264, -0.195)	0.166 (0.13, 0.201)	-0.131 (-0.169, -0.093)	-0.154 (-0.192, -0.116)
Precipitation	0.071 (0.044, 0.097)	-0.013 (-0.044, 0.018)	0.117 (0.09, 0.143)	-0.044 (-0.072, -0.016)	0.006 (-0.025, 0.037)	0.051 (0.026, 0.076)	0.015 (-0.014, 0.044)
PM$_{2.5}$	**-0.074 (-0.108, -0.04)**	0.023 (-0.003, 0.049)	-0.001 (-0.035, 0.034)	0.006 (-0.022, 0.035)	0.001 (-0.026, 0.027)	**-0.038 (-0.075, -0.001)**	**-0.053 (-0.091, -0.016)**
p-value (PM$_{2.5}$)	**2.3×10^{-5}**	0.09	0.97	0.66	0.97	**0.05**	**5.3×10^{-3}**
Conditional R^2	0.43	0.43	0.43	0.36	0.39	0.45	0.35
AIC	40626.59**	39176.03*	40887.40	41589.37	40350.55	39786.01**	41404.44**

	Common Yellowthroat	**Mourning Dove**	**Red-tailed Hawk**	**Downy Woodpecker**	**Ring-billed Gull**	**Swainson's Thrush**	**Pied-billed Grebe**
No. of detections	8,203	7,943	7,465	7,306	6,623	6,430	5,976
Intercept	-2.548 (-2.674, -2.423)	-2.928 (-3.059, -2.797)	-2.713 (-2.824, -2.603)	-2.697 (-2.811, -2.583)	-3.238 (-3.365, -3.111)	-3.704 (-3.851, -3.557)	-2.905 (-3.036, -2.774)
2016	-0.071 (-0.171, 0.028)	0.215 (0.115, 0.315)	0.067 (-0.03, 0.163)	0.158 (0.058, 0.258)	-0.149 (-0.251, -0.047)	-0.175 (-0.292, -0.057)	-0.098 (-0.206, 0.009)
2017	-0.164 (-0.263, -0.065)	-0.21 (-0.309, -0.111)	-0.163 (-0.258, -0.068)	-0.075 (-0.174, 0.023)	-0.076 (-0.173, 0.021)	-0.167 (-0.281, -0.053)	-0.443 (-0.551, -0.336)
2018	-0.184 (-0.281, -0.088)	-0.119 (-0.217, -0.022)	-0.146 (-0.239, -0.053)	0.101 (0.006, 0.197)	-0.199 (-0.296, -0.102)	0.052 (-0.058, 0.161)	-0.162 (-0.265, -0.059)
Barren	-0.337 (-0.459, -0.216)	-0.302 (-0.446, -0.157)	-0.889 (-1.052, -0.726)	-0.966 (-1.131, -0.8)	1.481 (1.375, 1.587)	-0.432 (-0.586, -0.278)	-1.395 (-1.596, -1.193)
Cultivated	0.416 (0.298, 0.534)	0.841 (0.729, 0.954)	0.804 (0.699, 0.909)	0.337 (0.216, 0.459)	0.517 (0.389, 0.646)	0.196 (0.051, 0.342)	-0.404 (-0.562, -0.246)
Forest	-1.345 (-1.484, -1.207)	-0.017 (-0.129, 0.094)	-0.531 (-0.647, -0.414)	0.163 (0.061, 0.265)	-0.574 (-0.728, -0.419)	0.867 (0.765, 0.969)	-1.429 (-1.608, -1.25)
Herbaceous	-0.439 (-0.601, -0.277)	0.096 (-0.067, 0.26)	0.012 (-0.136, 0.161)	0.079 (-0.067, 0.225)	0.563 (0.405, 0.72)	0.481 (0.314, 0.648)	-1.686 (-1.952, -1.42)
Water	-0.722 (-0.838, -0.606)	-0.14 (-0.247, -0.034)	-0.436 (-0.544, -0.329)	-0.6 (-0.717, -0.482)	1.225 (1.134, 1.316)	-0.907 (-1.056, -0.757)	0.411 (0.312, 0.51)
Shrubland	-0.883 (-1.057, -0.709)	0.461 (0.34, 0.582)	0.442 (0.325, 0.559)	-0.333 (-0.482, -0.183)	0.345 (0.196, 0.494)	-0.275 (-0.454, -0.096)	-0.361 (-0.528, -0.193)
Wetlands	1.437 (1.356, 1.517)	0.368 (0.273, 0.463)	0.595 (0.511, 0.679)	0.811 (0.725, 0.897)	1.296 (1.205, 1.388)	0.533 (0.431, 0.634)	1.316 (1.23, 1.402)
Day	-0.427 (-0.462, -0.392)	-0.174 (-0.209, -0.14)	0.162 (0.131, 0.193)	0.187 (0.154, 0.221)	0.419 (0.382, 0.456)	-1.172 (-1.219, -1.125)	0.441 (0.402, 0.479)
Day^2	-0.119 (-0.155, -0.083)	-0.025 (-0.061, 0.011)	0.213 (0.179, 0.246)	0.023 (-0.012, 0.058)	-0.047 (-0.085, -0.01)	0.152 (0.11, 0.195)	0.041 (0.002, 0.08)
Time	-0.286 (-0.319, -0.253)	-0.224 (-0.256, -0.192)	-0.113 (-0.145, -0.081)	-0.466 (-0.501, -0.431)	0.033 (-0.001, 0.066)	-0.283 (-0.32, -0.246)	-0.056 (-0.093, -0.019)
Duration	0.389 (0.356, 0.422)	0.213 (0.183, 0.242)	0.29 (0.263, 0.317)	0.475 (0.444, 0.506)	0.23 (0.198, 0.263)	0.485 (0.449, 0.521)	0.278 (0.244, 0.312)
Distance	0.183 (0.153, 0.213)	0.23 (0.204, 0.257)	0.393 (0.368, 0.417)	0.079 (0.049, 0.109)	0.062 (0.032, 0.092)	0.17 (0.136, 0.203)	0.165 (0.134, 0.195)
Temperature	-0.235 (-0.276, -0.194)	0.304 (0.269, 0.34)	0.101 (0.065, 0.136)	0.101 (0.063, 0.139)	0.119 (0.08, 0.158)	-0.356 (-0.404, -0.309)	0.208 (0.164, 0.251)
Precipitation	0.038 (0.009, 0.067)	0.004 (-0.033, 0.04)	-0.021 (-0.052, 0.01)	-0.017 (-0.049, 0.015)	0.01 (-0.018, 0.039)	0.002 (-0.039, 0.042)	0.039 (0.008, 0.071)
PM$_{2.5}$	0.005 (-0.031, 0.041)	0.002 (-0.024, 0.029)	**-0.071 (-0.105, -0.038)**	0.026 (-0.003, 0.056)	-0.018 (-0.049, 0.012)	0.002 (-0.047, 0.052)	-0.002 (-0.037, 0.033)
p-value (PM$_{2.5}$)	0.78	0.86	**3.4 x 10^{-5}**	0.08	0.24	0.92	0.91
Conditional R^2	0.51	0.45	0.34	0.39	0.43	0.56	0.46
AIC	36720.45	36457.11	38094.95**	36807.04*	35130.68	29538.71	30914.38

	Least Sandpiper	**Bushtit**	**Brown Creeper**	**Western Sandpiper**	**Pigeon Guillemot**	**Golden-crowned Kinglet**	**Yellow-rumped Warbler**
No. of detections	5,948	5,875	5,756	5653	5,423	5,384	5,363
Intercept	-2.939 (-3.076, -2.801)	-2.629 (-2.756, -2.502)	-3.304 (-3.442, -3.166)	-2.89 (-3.026, -2.755)	-3.3 (-3.443, -3.156)	-3.847 (-4.017, -3.677)	-4.135 (-4.289, -3.981)
2016	-0.271 (-0.377, -0.165)	-0.151 (-0.26, -0.042)	0.057 (-0.061, 0.175)	-0.539 (-0.647, -0.43)	-0.036 (-0.152, 0.08)	-0.04 (-0.158, 0.078)	-0.562 (-0.682, -0.443)
2017	-0.151 (-0.254, -0.048)	-0.252 (-0.357, -0.146)	-0.02 (-0.135, 0.094)	-0.224 (-0.326, -0.122)	0.176 (0.064, 0.288)	-0.511 (-0.63, -0.391)	-0.497 (-0.61, -0.384)
2018	-0.297 (-0.399, -0.195)	-0.059 (-0.161, 0.042)	0.243 (0.133, 0.354)	-0.389 (-0.49, -0.287)	-0.015 (-0.128, 0.098)	-0.267 (-0.381, -0.152)	-0.463 (-0.574, -0.351)
Barren	1.708 (1.605, 1.811)	-0.779 (-0.923, -0.635)	-0.688 (-0.851, -0.526)	1.933 (1.83, 2.036)	1.269 (1.159, 1.379)	-0.568 (-0.726, -0.411)	-0.3 (-0.47, -0.129)
Cultivated	-0.175 (-0.341, -0.009)	-0.706 (-0.88, -0.531)	0.013 (-0.142, 0.168)	-0.09 (-0.26, 0.08)	-0.223 (-0.406, -0.041)	-0.527 (-0.711, -0.343)	0.498 (0.361, 0.636)
Forest	-2.166 (-2.431, -1.9)	-0.562 (-0.682, -0.442)	1.292 (1.194, 1.39)	-1.732 (-1.972, -1.493)	0.485 (0.365, 0.604)	1.339 (1.233, 1.446)	0.382 (0.253, 0.512)
Herbaceous	0.478 (0.313, 0.643)	0.259 (0.117, 0.401)	0.865 (0.72, 1.01)	0.773 (0.614, 0.933)	0.869 (0.705, 1.033)	0.622 (0.466, 0.778)	0.475 (0.311, 0.64)
Water	0.846 (0.747, 0.946)	-1.062 (-1.196, -0.927)	-0.793 (-0.94, -0.646)	0.942 (0.841, 1.043)	1.647 (1.552, 1.743)	-0.76 (-0.902, -0.617)	-0.171 (-0.299, -0.043)
Shrubland	-0.023 (-0.199, 0.153)	-1.244 (-1.473, -1.015)	-0.492 (-0.689, -0.295)	-0.051 (-0.234, 0.131)	-0.485 (-0.721, -0.248)	0.033 (-0.142, 0.208)	1.074 (0.936, 1.212)
Wetlands	1.346 (1.253, 1.44)	0.163 (0.07, 0.257)	0.307 (0.202, 0.412)	1.252 (1.155, 1.35)	-0.489 (-0.629, -0.348)	-0.363 (-0.489, -0.236)	0.458 (0.343, 0.573)
Day	-0.391 (-0.434, -0.348)	-0.09 (-0.127, -0.053)	0.078 (0.04, 0.116)	-0.226 (-0.268, -0.183)	-0.479 (-0.523, -0.436)	0.54 (0.498, 0.582)	0.754 (0.713, 0.796)
Day^2	-0.568 (-0.612, -0.524)	0.024 (-0.014, 0.061)	0.007 (-0.032, 0.046)	-0.516 (-0.561, -0.472)	-0.313 (-0.357, -0.269)	0.254 (0.211, 0.297)	0.569 (0.527, 0.612)
Time	0.076 (0.042, 0.111)	-0.184 (-0.219, -0.148)	-0.388 (-0.427, -0.348)	0.069 (0.034, 0.105)	-0.081 (-0.117, -0.045)	-0.359 (-0.402, -0.317)	-0.3 (-0.341, -0.259)
Duration	0.382 (0.346, 0.418)	0.374 (0.341, 0.407)	0.487 (0.453, 0.521)	0.374 (0.339, 0.41)	0.152 (0.116, 0.187)	0.513 (0.475, 0.551)	0.456 (0.421, 0.49)
Distance	-0.111 (-0.151, -0.072)	0.138 (0.105, 0.171)	0.224 (0.193, 0.256)	-0.049 (-0.086, -0.011)	0.172 (0.14, 0.203)	0.265 (0.231, 0.299)	0.121 (0.089, 0.153)
Temperature	-0.033 (-0.076, 0.009)	0.142 (0.097, 0.187)	-0.049 (-0.096, -0.002)	-0.066 (-0.109, -0.023)	-0.211 (-0.259, -0.164)	-0.117 (-0.167, -0.067)	-0.307 (-0.352, -0.262)
Precipitation	0.011 (-0.024, 0.045)	0.029 (-0.004, 0.061)	-0.041 (-0.077, -0.004)	0.056 (0.025, 0.088)	-0.078 (-0.12, -0.036)	-0.002 (-0.036, 0.033)	-0.216 (-0.259, -0.174)
PM$_{2.5}$	-0.013 (-0.049, 0.023)	**-0.053 (-0.093, -0.013)**	-0.007 (-0.048, 0.034)	0.029 (-0.005, 0.063)	0.037 (-0.003, 0.076)	0.033 (-0.01, 0.076)	**0.079 (0.045, 0.112)**
p-value (PM$_{2.5}$)	0.47	**0.01**	0.73	0.09	0.07	0.14	**3.7 x 10^{-6}**
Conditional R^2	0.52	0.39	0.46	0.49	0.45	0.60	0.53
AIC	30475.88	32492.39**	30025.46	29827.43*	28763.18*	26628.52*	26324.52**

	Western Wood-Pewee	**Heermann's Gull**	**Turkey Vulture**	**Black-headed Grosbeak**	**Yellow Warbler**	**Brown-headed Cowbird**	**Orange-crowned Warbler**
No. of detections	5,320	5,218	5,195	4,855	4,668	4,622	4,444
Intercept	-3.343 (-3.498, -3.188)	-2.63 (-2.763, -2.498)	-3.085 (-3.224, -2.945)	-3.49 (-3.638, -3.342)	-3.401 (-3.545, -3.257)	-3.587 (-3.728, -3.447)	-3.596 (-3.745, -3.447)
2016	0.193 (0.069, 0.318)	-0.411 (-0.522, -0.3)	-0.049 (-0.166, 0.068)	0.016 (-0.108, 0.139)	0.096 (-0.022, 0.214)	-0.037 (-0.159, 0.085)	-0.141 (-0.263, -0.018)
2017	-0.069 (-0.192, 0.054)	-0.285 (-0.392, -0.177)	-0.079 (-0.195, 0.037)	-0.226 (-0.349, -0.103)	-0.04 (-0.156, 0.075)	-0.182 (-0.3, -0.063)	0.062 (-0.055, 0.179)
2018	0.045 (-0.075, 0.164)	-0.781 (-0.892, -0.67)	0.044 (-0.068, 0.155)	0.063 (-0.053, 0.18)	-0.076 (-0.189, 0.037)	0.083 (-0.03, 0.196)	0.041 (-0.074, 0.155)
Barren	-2.161 (-2.512, -1.81)	0.93 (0.821, 1.039)	0.04 (-0.102, 0.182)	-1.337 (-1.578, -1.095)	-0.782 (-0.982, -0.583)	0.401 (0.262, 0.539)	-0.387 (-0.545, -0.229)
Cultivated	0.895 (0.76, 1.029)	-0.668 (-0.875, -0.461)	0.582 (0.455, 0.709)	0.5 (0.358, 0.642)	0.345 (0.202, 0.488)	0.482 (0.338, 0.627)	-0.062 (-0.224, 0.099)
Forest	0.155 (0.028, 0.282)	-0.538 (-0.687, -0.39)	-0.118 (-0.242, 0.007)	0.416 (0.301, 0.53)	-0.521 (-0.672, -0.369)	-0.779 (-0.935, -0.624)	0.071 (-0.056, 0.197)
Herbaceous	0.104 (-0.088, 0.296)	0.897 (0.751, 1.044)	0.018 (-0.157, 0.193)	0.061 (-0.135, 0.257)	0.497 (0.335, 0.66)	0.528 (0.356, 0.701)	1.019 (0.875, 1.163)
Water	-0.199 (-0.336, -0.063)	1.455 (1.364, 1.546)	-0.121 (-0.239, -0.004)	-0.768 (-0.927, -0.608)	-0.155 (-0.288, -0.022)	-0.124 (-0.259, 0.011)	-0.594 (-0.736, -0.452)
Shrubland	0.329 (0.186, 0.472)	-1.11 (-1.371, -0.848)	0.412 (0.264, 0.561)	0.141 (-0.025, 0.308)	0.098 (-0.058, 0.255)	-0.078 (-0.249, 0.093)	0.102 (-0.065, 0.269)
Wetlands	0.853 (0.746, 0.96)	-0.757 (-0.904, -0.609)	0.507 (0.405, 0.609)	0.142 (0.026, 0.259)	1.186 (1.087, 1.286)	0.918 (0.815, 1.021)	0.291 (0.181, 0.402)
Day	-1.279 (-1.342, -1.216)	0.183 (0.141, 0.225)	-0.145 (-0.184, -0.107)	-1.48 (-1.552, -1.409)	-0.445 (-0.488, -0.401)	-1.187 (-1.246, -1.128)	0.203 (0.162, 0.244)
Day^2	-0.623 (-0.678, -0.567)	-0.204 (-0.248, -0.16)	-0.137 (-0.178, -0.096)	-0.391 (-0.448, -0.334)	-0.114 (-0.158, -0.07)	-0.095 (-0.146, -0.045)	-0.006 (-0.048, 0.037)
Time	-0.299 (-0.338, -0.26)	0.006 (-0.031, 0.043)	0.038 (0.002, 0.074)	-0.46 (-0.501, -0.419)	-0.459 (-0.5, -0.417)	-0.353 (-0.393, -0.313)	-0.535 (-0.58, -0.49)
Duration	0.323 (0.289, 0.358)	0.135 (0.095, 0.174)	0.284 (0.251, 0.317)	0.397 (0.362, 0.431)	0.378 (0.344, 0.411)	0.318 (0.285, 0.351)	0.408 (0.375, 0.44)
Distance	0.248 (0.217, 0.278)	0.149 (0.116, 0.182)	0.25 (0.221, 0.278)	-0.007 (-0.045, 0.03)	0.16 (0.128, 0.191)	0.146 (0.114, 0.179)	0.09 (0.055, 0.126)
Temperature	-0.002 (-0.045, 0.042)	-0.306 (-0.355, -0.256)	-0.455 (-0.501, -0.408)	-0.104 (-0.15, -0.057)	-0.018 (-0.062, 0.026)	-0.011 (-0.056, 0.034)	-0.297 (-0.345, -0.248)
Precipitation	0.005 (-0.05, 0.06)	-0.014 (-0.047, 0.018)	0.001 (-0.03, 0.032)	0.043 (-0.005, 0.092)	0.041 (0.002, 0.08)	0.013 (-0.038, 0.063)	0.047 (0.015, 0.08)
$PM_{2.5}$	0.027 (-0.005, 0.059)	**-0.094 (-0.149, -0.038)**	**-0.107 (-0.157, -0.057)**	**0.072 (0.034, 0.111)**	**0.064 (0.031, 0.096)**	**0.061 (0.024, 0.098)**	**0.083 (0.048, 0.119)**
p-value ($PM_{2.5}$)	0.09	**8.8 x 10^{-4}**	**3.1 x 10^{-5}**	**2.1 x 10^{-4}**	**1.3 x 10^{-4}**	**1.3 x 10^{-3}**	**4.6 x 10^{-6}**
Conditional R^2	0.61	0.46	0.42	0.57	0.45	0.48	0.43
AIC	26015.99*	27937.20**	30087.90**	25046.04**	26706.13**	25990.05**	26220.43**

	Western Tanager	**Wood Duck**	**Marsh Wren**	**Greater Yellowlegs**	**Tree Swallow**	**Gadwall**	**Pelagic Cormorant**
No. of detections	4,424	4,348	4,306	4,304	4,133	4,089	4,005
Intercept	-3.249 (-3.401, -3.097)	-3.634 (-3.789, -3.479)	-3.821 (-3.977, -3.666)	-3.561 (-3.718, -3.403)	-3.881 (-4.046, -3.716)	-4.084 (-4.26, -3.908)	-3.711 (-3.872, -3.55)
Year_2016	-0.222 (-0.345, -0.099)	0.08 (-0.051, 0.212)	-0.169 (-0.292, -0.046)	-0.061 (-0.181, 0.06)	0.017 (-0.118, 0.152)	-0.276 (-0.407, -0.145)	-0.068 (-0.197, 0.061)
Year_2017	-0.339 (-0.459, -0.218)	0.019 (-0.109, 0.146)	-0.417 (-0.539, -0.295)	-0.141 (-0.259, -0.023)	-0.314 (-0.448, -0.179)	-0.227 (-0.352, -0.103)	0.104 (-0.02, 0.228)
Year_2018	-0.069 (-0.184, 0.045)	0.18 (0.056, 0.305)	-0.384 (-0.503, -0.265)	-0.156 (-0.273, -0.039)	-0.445 (-0.578, -0.312)	-0.17 (-0.292, -0.047)	-0.172 (-0.298, -0.047)
Barren	-1.229 (-1.457, -1.002)	-2.648 (-3.085, -2.21)	0.397 (0.245, 0.549)	0.945 (0.819, 1.071)	-0.122 (-0.315, 0.071)	-0.438 (-0.632, -0.243)	0.484 (0.347, 0.621)
Cultivated	0.264 (0.121, 0.408)	-0.088 (-0.261, 0.085)	-0.561 (-0.779, -0.342)	-0.493 (-0.694, -0.292)	0.505 (0.342, 0.667)	-0.646 (-0.86, -0.433)	-0.683 (-0.913, -0.452)
Forest	0.789 (0.679, 0.898)	-0.673 (-0.844, -0.503)	-1.526 (-1.761, -1.291)	-1.674 (-1.943, -1.404)	-0.731 (-0.901, -0.561)	-1.599 (-1.866, -1.332)	0.63 (0.502, 0.758)
Herbaceous	0.211 (0.036, 0.386)	-2.175 (-2.595, -1.754)	-0.031 (-0.244, 0.182)	-0.113 (-0.338, 0.112)	-0.196 (-0.43, 0.038)	-1.329 (-1.648, -1.011)	0.475 (0.295, 0.656)
Water	-0.837 (-0.993, -0.68)	0.134 (0.003, 0.264)	0.163 (0.03, 0.297)	0.623 (0.505, 0.741)	0.355 (0.216, 0.494)	0.852 (0.74, 0.965)	1.524 (1.422, 1.627)
Shrubland	0.179 (0.022, 0.335)	-0.389 (-0.587, -0.191)	-0.636 (-0.871, -0.4)	0.066 (-0.12, 0.253)	0.027 (-0.166, 0.221)	-0.487 (-0.713, -0.26)	-0.531 (-0.775, -0.287)
Wetlands	-0.373 (-0.5, -0.246)	1.813 (1.717, 1.909)	2.079 (1.981, 2.176)	1.814 (1.714, 1.914)	1.613 (1.502, 1.724)	1.79 (1.688, 1.892)	-0.328 (-0.476, -0.18)
Day	-0.625 (-0.672, -0.578)	0.216 (0.173, 0.26)	-0.121 (-0.163, -0.079)	0.117 (0.071, 0.163)	-1.883 (-1.978, -1.788)	0.392 (0.346, 0.437)	0.116 (0.071, 0.16)
Day^2	-0.225 (-0.272, -0.178)	-0.005 (-0.05, 0.04)	0.269 (0.226, 0.312)	-0.332 (-0.379, -0.284)	-0.403 (-0.472, -0.334)	0.134 (0.088, 0.18)	-0.081 (-0.129, -0.034)
Time	-0.42 (-0.462, -0.378)	-0.1 (-0.144, -0.057)	-0.187 (-0.229, -0.144)	0.045 (0.005, 0.085)	-0.141 (-0.184, -0.099)	0.03 (-0.013, 0.074)	0.073 (0.033, 0.113)
Duration	0.401 (0.367, 0.435)	0.373 (0.337, 0.41)	0.367 (0.33, 0.404)	0.334 (0.296, 0.372)	0.331 (0.292, 0.37)	0.258 (0.217, 0.299)	0.18 (0.141, 0.219)
Distance	0.126 (0.093, 0.159)	0.193 (0.16, 0.226)	0.084 (0.045, 0.123)	-0.046 (-0.087, -0.005)	0.186 (0.15, 0.221)	-0.037 (-0.081, 0.006)	0.173 (0.139, 0.206)
Temperature	-0.262 (-0.308, -0.216)	0.164 (0.114, 0.214)	0.065 (0.013, 0.116)	0.148 (0.1, 0.196)	-0.155 (-0.207, -0.102)	0.134 (0.082, 0.186)	-0.4 (-0.456, -0.345)
Precipitation	-0.056 (-0.102, -0.01)	0.071 (0.035, 0.107)	0.05 (0.012, 0.087)	0.037 (0.001, 0.073)	0.072 (0.018, 0.126)	0.058 (0.021, 0.094)	0.044 (0.013, 0.076)
$PM_{2.5}$	**0.128 (0.097, 0.159)**	-0.01 (-0.052, 0.031)	**-0.082 (-0.137, -0.026)**	**-0.087 (-0.134, -0.039)**	-0.014 (-0.073, 0.045)	0.014 (-0.029, 0.057)	-0.014 (-0.067, 0.04)
p-value ($PM_{2.5}$)	**3.8 x 10^{-16}**	0.62	**3.9 x 10^{-3}**	**3.4 x 10^{-4}**	0.64	0.52	0.62
Conditional R^2	0.48	0.50	0.48	0.49	0.64	0.53	0.47
AIC	25677.79**	24213.14	24116.40**	25035.76**	21483.79	23072.43	24319.52

	California Quail	**Green-winged Teal**	**Brewer's Blackbird**	**Spotted Sandpiper**	**Rhinoceros Auklet**	**American Coot**	**Northern Harrier**
No. of detections	3,839	3,827	3,806	3,473	3,463	3,437	3,318
Intercept	-5.359 (-5.707, -5.011)	-4.131 (-4.301, -3.961)	-4.112 (-4.288, -3.935)	-3.423 (-3.582, -3.264)	-4.6 (-4.817, -4.382)	-4.037 (-4.205, -3.869)	-4.072 (-4.239, -3.904)
2016	0.228 (0.085, 0.37)	-0.201 (-0.329, -0.074)	-0.005 (-0.135, 0.125)	0.118 (-0.006, 0.241)	0.027 (-0.108, 0.162)	-0.476 (-0.614, -0.338)	-0.238 (-0.378, -0.097)
2017	-0.032 (-0.169, 0.105)	-0.179 (-0.301, -0.058)	-0.091 (-0.215, 0.034)	-0.225 (-0.35, -0.1)	-0.156 (-0.291, -0.021)	-0.297 (-0.424, -0.171)	-0.203 (-0.339, -0.068)
2018	0.137 (0.002, 0.272)	-0.313 (-0.435, -0.191)	-0.153 (-0.277, -0.028)	-0.07 (-0.19, 0.05)	-0.191 (-0.325, -0.057)	-0.223 (-0.348, -0.099)	-0.168 (-0.301, -0.036)
Barren	-0.025 (-0.231, 0.181)	0.591 (0.443, 0.739)	-0.086 (-0.279, 0.107)	0.117 (-0.038, 0.271)	0.725 (0.581, 0.869)	-1.353 (-1.657, -1.049)	1.214 (1.063, 1.364)
Cultivated	0.46 (0.31, 0.61)	-0.073 (-0.258, 0.111)	1.248 (1.121, 1.375)	0.209 (0.043, 0.376)	0.184 (-0.019, 0.387)	-0.066 (-0.259, 0.128)	0.742 (0.582, 0.902)
Forest	-0.253 (-0.423, -0.082)	-1.551 (-1.832, -1.27)	-1.512 (-1.765, -1.258)	-0.682 (-0.863, -0.501)	0.405 (0.254, 0.557)	-1.405 (-1.666, -1.144)	-1.721 (-2.03, -1.413)
Herbaceous	0.328 (0.121, 0.535)	0.153 (-0.051, 0.357)	-0.254 (-0.49, -0.018)	0.004 (-0.205, 0.213)	1.237 (1.062, 1.411)	-0.093 (-0.311, 0.125)	0.567 (0.357, 0.776)
Water	-0.219 (-0.364, -0.073)	0.952 (0.836, 1.068)	0.642 (0.526, 0.757)	0.627 (0.509, 0.746)	1.63 (1.513, 1.747)	0.934 (0.816, 1.052)	-0.067 (-0.227, 0.094)
Shrubland	0.383 (0.236, 0.53)	0.241 (0.057, 0.424)	0.062 (-0.098, 0.222)	0.388 (0.227, 0.549)	-0.942 (-1.27, -0.615)	0.182 (0.003, 0.361)	0.291 (0.1, 0.482)
Wetlands	0.158 (0.015, 0.3)	1.533 (1.422, 1.644)	0.841 (0.727, 0.955)	0.476 (0.358, 0.594)	-0.49 (-0.674, -0.307)	1.426 (1.315, 1.536)	1.554 (1.439, 1.669)
Day	0.066 (0.019, 0.113)	1.248 (1.176, 1.319)	-0.014 (-0.057, 0.029)	-0.634 (-0.691, -0.576)	-0.294 (-0.343, -0.245)	0.675 (0.625, 0.725)	0.42 (0.371, 0.469)
Day^2	0.169 (0.12, 0.219)	-0.241 (-0.3, -0.181)	0.124 (0.079, 0.169)	-0.48 (-0.535, -0.424)	-0.027 (-0.078, 0.024)	0.191 (0.142, 0.24)	0.129 (0.079, 0.179)
Time	-0.203 (-0.247, -0.159)	-0.033 (-0.077, 0.011)	-0.039 (-0.079, 0.001)	-0.087 (-0.128, -0.046)	-0.092 (-0.136, -0.048)	0.021 (-0.025, 0.067)	0.016 (-0.031, 0.063)
Duration	0.263 (0.223, 0.304)	0.288 (0.247, 0.328)	0.023 (-0.021, 0.066)	0.286 (0.25, 0.323)	0.228 (0.186, 0.271)	0.13 (0.088, 0.172)	0.299 (0.261, 0.337)
Distance	0.073 (0.036, 0.109)	-0.028 (-0.07, 0.014)	0.189 (0.158, 0.221)	-0.025 (-0.064, 0.015)	0.283 (0.247, 0.319)	0.183 (0.148, 0.219)	0.306 (0.274, 0.339)
Temperature	0.188 (0.142, 0.235)	0.21 (0.159, 0.261)	0.218 (0.173, 0.262)	0.196 (0.149, 0.242)	-0.245 (-0.303, -0.186)	0.354 (0.303, 0.404)	-0.048 (-0.104, 0.007)
Precipitation	-0.29 (-0.378, -0.202)	0.066 (0.033, 0.098)	-0.018 (-0.064, 0.027)	0.083 (0.04, 0.126)	-0.079 (-0.128, -0.03)	0.063 (0.024, 0.102)	-0.008 (-0.047, 0.032)
$PM_{2.5}$	**0.031 (0.001, 0.061)**	-0.036 (-0.077, 0.004)	-0.015 (-0.048, 0.017)	-0.035 (-0.074, 0.005)	0.014 (-0.042, 0.069)	0.009 (-0.03, 0.047)	**-0.08 (-0.138, -0.023)**
p-value ($PM_{2.5}$)	**0.04**	0.08	0.35	0.08	0.63	066	**6.1×10^{-3}**
Conditional R^2	0.68	0.58	0.47	0.43	0.58	0.49	0.49
AIC	20817.77*	22113.34*	23394.58	23000.83*	20343.71	20988.45	20544.70**

APPENDIX D

This appendix includes additional information about the covariates considered in the analysis presented in chapter 3. Before running our models, we assessed the correlation between all numeric variables in our dataset. The correlation matrix and a visualization of the matrix are provided in this appendix.

Table A.2: A matrix showing the correlation between all numeric variables included in our model.

	Day	**Time**	**Duration**	**Distance**	**Temperature**	**Precipitation**	**PM$_{2.5}$**
Day	1	0.013	0.006	0.009	-0.39	0.185	0.023
Time	0.013	1	-0.191	-0.072	-0.05	0.034	-0.023
Duration	0.006	-0.191	1	0.316	-0.014	-0.017	-0.013
Distance	0.009	-0.072	0.316	1	-0.009	-0.008	0
Temperature	-0.39	-0.05	-0.014	-0.009	1	-0.267	0.295
Precipitation	0.185	0.034	-0.017	-0.008	-0.267	1	-0.113
PM$_{2.5}$	0.023	-0.023	-0.013	0	0.295	-0.113	1

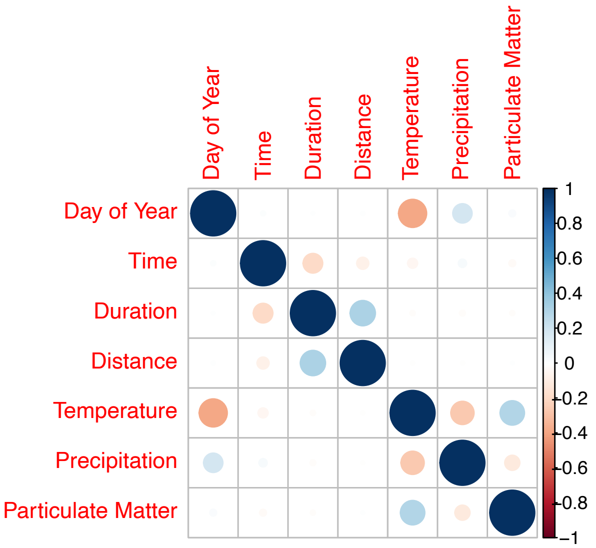

Figure A.1: Visualization of the correlation matrix created using the *corrplot* package[1] in R.

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[1] Taiyun Wei and Viliam Simko (2017). R package "corrplot": Visualization of a Correlation Matrix (Version 0.84). Available from https://github.com/taiyun/corrplot

APPENDIX E

This appendix includes additional information about the covariates considered in the analysis presented in chapter 5. We were concerned that some of the effects on detection in our occupancy models may be highly correlated. We used a correlation matrix to examine the relationship between numeric effects on detection, which we have provided here. R^2 values above .5 are bolded. As expected, there is a slight positive correlation between daily mean air temperature and day of year and between percent change in human mobility and day of year.

	Day	Time	Temperature	Precipitation	Mobility	$PM_{2.5}$
Day	1.000	-0.029	**0.662**	0.062	**0.573**	-0.430
Time	-0.029	1.000	-0.038	0.024	-0.045	0.028
Temperature	**0.662**	-0.038	1.000	-0.184	0.373	-0.078
Precipitation	0.062	0.024	-0.184	1.000	-0.094	-0.328
Mobility	**0.573**	-0.045	0.373	-0.094	1.000	-0.325
$PM_{2.5}$	-0.430	0.028	-0.078	-0.328	-0.325	1.000

APPENDIX F

This appendix includes complete model results for the analysis presented in chapter 5.

The following tables present complete model results for each of the 46 study species included in our analysis. Estimates for intercepts and effects on both occupancy and detection are provided along with 95% confidence intervals. Effects that meet our threshold for statistical significance ($p < 0.05$) are bolded. The color coding indicates whether the information is relevant to the observation (blue) or state process (orange).

Species	**American Crow**	**American Goldfinch**	**American Robin**	**Anna's Hummingbird**	**Bald Eagle**	**Band-tailed Pigeon**
Intercept (Ψ)	3.07 (2.31, 3.83)	-0.51 (-0.86, -0.15)	2.34 (1.78, 2.9)	1.04 (0.67, 1.4)	-0.52 (-0.96, -0.08)	-1.45 (-1.9, -1)
Highly Developed	**-1.39 (-2.38, -0.41)**	**-0.7 (-1.35, -0.05)**	-0.71 (-1.53, 0.12)	0.31 (-0.35, 0.98)	-0.02 (-0.76, 0.72)	-0.69 (-1.63, 0.25)
Natural Areas	**-1.89 (-2.94, -0.84)**	0.51 (-0.24, 1.27)	-0.41 (-1.47, 0.65)	-0.65 (-1.38, 0.08)	0.66 (-0.31, 1.63)	0.64 (-0.21, 1.5)
Canopy Cover	-0.09 (-0.51, 0.33)	-0.19 (-0.48, 0.11)	0.31 (-0.19, 0.81)	0.25 (-0.07, 0.57)	-0.14 (-0.5, 0.23)	0.33 (-0.03, 0.69)
Detection (p)	0.35 (0.25, 0.46)	-1.53 (-1.73, -1.33)	-0.24 (-0.34, -0.14)	-0.38 (-0.48, -0.27)	-2.64 (-2.94, -2.34)	-1.07 (-1.37, -0.76)
Day of Year	**0.31 (0.22, 0.41)**	**-0.52 (-0.68, -0.36)**	0.07 (-0.02, 0.16)	**0.22 (0.12, 0.32)**	-0.17 (-0.44, 0.1)	**0.48 (0.19, 0.77)**
Day of Year^2	0.04 (-0.01, 0.1)	0.04 (-0.06, 0.14)	**-0.14 (-0.19, -0.08)**	**-0.09 (-0.15, -0.03)**	-0.07 (-0.24, 0.1)	**-0.51 (-0.71, -0.3)**
Weekend	**-0.22 (-0.35, -0.09)**	0.15 (-0.08, 0.39)	0.01 (-0.12, 0.13)	0.01 (-0.13, 0.14)	0.28 (-0.07, 0.63)	-0.2 (-0.6, 0.2)
Time	**-0.34 (-0.41, -0.28)**	-0.05 (-0.17, 0.07)	**-0.4 (-0.47, -0.34)**	**-0.18 (-0.24, -0.11)**	**0.34 (0.13, 0.55)**	-0.08 (-0.27, 0.12)
Time^2	**0.15 (0.09, 0.21)**	**-0.15 (-0.27, -0.03)**	**0.45 (0.39, 0.52)**	**0.13 (0.07, 0.19)**	-0.06 (-0.24, 0.12)	**-0.35 (-0.57, -0.13)**
Temperature	0.02 (-0.06, 0.1)	0.11 (-0.02, 0.23)	**-0.1 (-0.18, -0.03)**	-0.08 (-0.16, 0)	-0.08 (-0.31, 0.15)	**-0.31 (-0.55, -0.08)**
Precipitation	-0.06 (-0.12, 0)	-0.04 (-0.15, 0.07)	0.01 (-0.05, 0.07)	-0.07 (-0.13, 0)	-0.02 (-0.2, 0.15)	**0.15 (0.01, 0.3)**
Mobility	**-0.44 (-0.51, -0.37)**	**0.55 (0.44, 0.65)**	-0.01 (-0.07, 0.06)	-0.08 (-0.15, 0)	0.16 (-0.03, 0.35)	**0.2 (0.02, 0.37)**
PM$_{2.5}$	0.05 (-0.02, 0.12)	-0.04 (-0.16, 0.08)	0.06 (0, 0.13)	0.01 (-0.06, 0.08)	0.05 (-0.14, 0.23)	0.21 (0, 0.43)

Species	**Barn Swallow**	**Bewick's Wren**	**Black-capped Chickadee**	**Black-headed Grosbeak**	**Brown-headed Cowbird**	**Bushtit**
Intercept (Ψ)	-2.12 (-2.72, -1.52)	0.16 (-0.16, 0.48)	2.61 (1.94, 3.29)	-0.92 (-1.32, -0.53)	-1.47 (-1.94, -0.99)	0.22 (-0.14, 0.59)
Highly Developed	-0.59 (-1.73, 0.54)	-0.06 (-0.62, 0.5)	-0.65 (-1.62, 0.31)	**-0.93 (-1.77, -0.09)**	-0.73 (-1.68, 0.22)	0.66 (-0.06, 1.37)
Natural Areas	0.89 (-0.11, 1.9)	-0.56 (-1.25, 0.12)	**-2.25 (-3.16, -1.35)**	0.69 (-0.11, 1.49)	0.63 (-0.28, 1.54)	**-0.92 (-1.74, -0.09)**
Canopy Cover	-0.26 (-0.74, 0.21)	0.13 (-0.14, 0.4)	0.25 (-0.17, 0.68)	0.18 (-0.15, 0.51)	-0.01 (-0.39, 0.37)	0.09 (-0.23, 0.41)
Detection (p)	-2.02 (-2.5, -1.54)	-0.74 (-0.87, -0.6)	-0.11 (-0.21, -0.01)	-1.27 (-1.53, -1.01)	-1.81 (-2.2, -1.42)	-1.67 (-1.83, -1.5)
Day of Year	0 (-0.39, 0.38)	-0.05 (-0.18, 0.08)	**0.26 (0.16, 0.35)**	**0.79 (0.51, 1.06)**	**1.01 (0.7, 1.33)**	-0.04 (-0.2, 0.12)
Day of Year^2	**-0.36 (-0.6, -0.12)**	0.02 (-0.05, 0.1)	**0.14 (0.08, 0.2)**	**-0.94 (-1.15, -0.73)**	**-0.25 (-0.46, -0.05)**	0.02 (-0.07, 0.12)
Weekend	0.35 (-0.15, 0.85)	-0.17 (-0.33, 0)	-0.12 (-0.24, 0)	0.25 (-0.06, 0.57)	0.16 (-0.23, 0.55)	0.01 (-0.2, 0.21)
Time	0.17 (-0.1, 0.45)	**-0.25 (-0.34, -0.17)**	**-0.27 (-0.33, -0.21)**	0.03 (-0.13, 0.2)	**-0.67 (-0.95, -0.39)**	**0.23 (0.12, 0.34)**
Time^2	0 (-0.22, 0.23)	0.04 (-0.04, 0.11)	**0.12 (0.06, 0.18)**	-0.06 (-0.21, 0.09)	-0.21 (-0.47, 0.04)	**-0.15 (-0.25, -0.05)**
Temperature	0.09 (-0.24, 0.41)	0.06 (-0.05, 0.16)	**-0.11 (-0.19, -0.03)**	0.08 (-0.1, 0.26)	-0.06 (-0.28, 0.16)	0.03 (-0.1, 0.17)
Precipitation	0.14 (-0.07, 0.35)	0.01 (-0.07, 0.09)	-0.01 (-0.07, 0.05)	**0.18 (0.05, 0.31)**	**-0.25 (-0.45, -0.04)**	-0.08 (-0.19, 0.03)
Mobility	**0.71 (0.42, 1.01)**	**-0.11 (-0.21, -0.01)**	**-0.28 (-0.34, -0.21)**	**0.5 (0.36, 0.64)**	**-0.22 (-0.43, -0.02)**	-0.01 (-0.14, 0.12)
PM$_{2.5}$	-0.03 (-0.3, 0.24)	0.09 (0, 0.17)	0 (-0.07, 0.06)	0.11 (-0.09, 0.3)	-0.16 (-0.39, 0.07)	-0.02 (-0.12, 0.09)

Species	**California Scrub-jay**	**Canada Goose**	**Chestnut-backed Chickadee**	**Dark-eyed Junco**	**Downy Woodpecker**	**Eurasian Collared-Dove**
Intercept (Ψ)	-1.43 (-1.86, -1.01)	-0.94 (-1.38, -0.51)	-0.15 (-0.48, 0.18)	1.98 (1.45, 2.51)	-0.63 (-1.05, -0.2)	-1.66 (-2.23, -1.08)
Highly Developed	0.55 (-0.11, 1.21)	-0.47 (-1.24, 0.29)	-0.33 (-0.92, 0.25)	-0.34 (-1.13, 0.45)	**-1.03 (-1.88, -0.17)**	-0.16 (-1.14, 0.83)
Natural Areas	0.17 (-0.75, 1.09)	**1.46 (0.55, 2.36)**	**-1 (-1.76, -0.24)**	-0.71 (-1.69, 0.27)	-0.22 (-1.16, 0.71)	0.05 (-1.09, 1.18)
Canopy Cover	-0.36 (-0.74, 0.01)	-0.32 (-0.69, 0.04)	**0.37 (0.08, 0.66)**	0.3 (-0.13, 0.72)	**0.43 (0.06, 0.81)**	-0.27 (-0.77, 0.22)
Detection (p)	-1.79 (-2.1, -1.47)	-2.43 (-2.75, -2.11)	-1.06 (-1.22, -0.89)	0.03 (-0.07, 0.12)	-2.52 (-2.87, -2.18)	-3.2 (-3.77, -2.64)
Day of Year	-0.1 (-0.33, 0.12)	**-0.72 (-0.98, -0.45)**	0.03 (-0.11, 0.17)	**0.35 (0.26, 0.44)**	-0.08 (-0.36, 0.21)	**-1.54 (-1.89, -1.2)**
Day of Year^2	0.14 (0, 0.28)	0.01 (-0.16, 0.18)	**0.15 (0.06, 0.23)**	0.01 (-0.04, 0.07)	0.16 (-0.01, 0.34)	**0.3 (0.11, 0.49)**
Weekend	0.24 (-0.08, 0.56)	-0.02 (-0.38, 0.34)	-0.01 (-0.21, 0.18)	-0.08 (-0.2, 0.04)	0.16 (-0.23, 0.55)	**0.51 (0.08, 0.95)**
Time	**-0.31 (-0.48, -0.15)**	**0.27 (0.07, 0.46)**	**0.13 (0.03, 0.22)**	**-0.22 (-0.28, -0.15)**	**-0.34 (-0.56, -0.11)**	**-0.37 (-0.69, -0.05)**
Time^2	-0.1 (-0.28, 0.09)	-0.09 (-0.25, 0.08)	**-0.15 (-0.25, -0.06)**	0.05 (-0.01, 0.11)	-0.01 (-0.21, 0.19)	-0.15 (-0.46, 0.17)
Temperature	-0.1 (-0.28, 0.09)	0.09 (-0.14, 0.31)	-0.02 (-0.14, 0.1)	**-0.21 (-0.29, -0.14)**	0.06 (-0.18, 0.29)	**0.7 (0.5, 0.9)**
Precipitation	-0.12 (-0.3, 0.05)	-0.11 (-0.3, 0.08)	**0.11 (0.03, 0.2)**	0.01 (-0.04, 0.07)	0.09 (-0.09, 0.26)	0 (-0.23, 0.22)
Mobility	0.04 (-0.12, 0.21)	**0.33 (0.17, 0.49)**	**0.37 (0.27, 0.46)**	**-0.15 (-0.22, -0.09)**	**0.24 (0.06, 0.42)**	**1.14 (0.86, 1.42)**
PM$_{2.5}$	-0.02 (-0.17, 0.14)	-0.02 (-0.19, 0.15)	**0.12 (0.02, 0.22)**	**0.1 (0.04, 0.17)**	-0.08 (-0.29, 0.13)	-0.45 (-0.67, -0.23)

Species	**European Starling**	**Glaucous-winged Gull**	**Golden-crowned Kinglet**	**Golden-crowned Sparrow**	**Great Blue Heron**	**House Finch**
Intercept (Ψ)	-0.13 (-0.45, 0.2)	-2.09 (-2.59, -1.59)	-1.43 (-1.89, -0.97)	-0.58 (-0.98, -0.18)	-1.4 (-1.85, -0.94)	0.83 (0.47, 1.18)
Highly Developed	**0.65 (0.05, 1.26)**	**0.78 (0.02, 1.55)**	0.45 (-0.32, 1.23)	-0.56 (-1.25, 0.13)	-0.47 (-1.33, 0.38)	0.47 (-0.22, 1.15)
Natural Areas	0.54 (-0.18, 1.25)	0.61 (-0.3, 1.53)	-0.56 (-1.63, 0.51)	-0.57 (-1.48, 0.35)	0.75 (-0.18, 1.67)	-0.57 (-1.25, 0.1)
Canopy Cover	**-0.3 (-0.58, -0.03)**	0.1 (-0.25, 0.46)	**0.55 (0.18, 0.92)**	-0.28 (-0.63, 0.07)	0.04 (-0.33, 0.42)	-0.28 (-0.56, 0)
Detection (p)	-1.04 (-1.18, -0.89)	-1.28 (-1.54, -1.02)	-1.52 (-1.84, -1.21)	-4.4 (-5.12, -3.68)	-1.52 (-1.88, -1.17)	-0.32 (-0.43, -0.21)
Day of Year	**-0.19 (-0.31, -0.07)**	**0.34 (0.06, 0.61)**	-0.11 (-0.4, 0.19)	**-5.9 (-7.31, -4.5)**	0.26 (-0.04, 0.56)	**0.22 (0.12, 0.31)**
Day of Year^2	**-0.1 (-0.18, -0.03)**	**0.16 (0.02, 0.31)**	**-0.23 (-0.41, -0.05)**	**-2.31 (-3, -1.61)**	-0.05 (-0.24, 0.15)	0.05 (-0.01, 0.11)
Weekend	0.14 (-0.03, 0.31)	-0.1 (-0.43, 0.23)	-0.17 (-0.56, 0.22)	0.15 (-0.19, 0.49)	0.18 (-0.24, 0.6)	0.06 (-0.07, 0.2)
Time	**-0.24 (-0.32, -0.15)**	**0.52 (0.33, 0.72)**	0.13 (-0.06, 0.32)	-0.1 (-0.3, 0.1)	**0.93 (0.67, 1.19)**	**-0.25 (-0.32, -0.19)**
Time^2	0.01 (-0.07, 0.1)	**-0.19 (-0.35, -0.04)**	**-0.3 (-0.51, -0.1)**	-0.16 (-0.35, 0.04)	**-0.77 (-0.99, -0.56)**	0.02 (-0.05, 0.08)
Temperature	**0.13 (0.04, 0.23)**	-0.14 (-0.36, 0.08)	-0.04 (-0.28, 0.2)	-0.17 (-0.41, 0.08)	-0.01 (-0.25, 0.24)	-0.03 (-0.1, 0.05)
Precipitation	0.03 (-0.05, 0.12)	0 (-0.19, 0.18)	**0.21 (0.06, 0.37)**	0.03 (-0.14, 0.21)	-0.04 (-0.26, 0.18)	**-0.08 (-0.15, -0.02)**
Mobility	**0.28 (0.19, 0.37)**	-0.18 (-0.43, 0.07)	0.16 (-0.08, 0.4)	0.12 (-0.06, 0.3)	**-0.29 (-0.54, -0.04)**	**-0.13 (-0.2, -0.05)**
PM$_{2.5}$	-0.01 (-0.11, 0.08)	0.13 (-0.03, 0.3)	**0.21 (0.02, 0.39)**	0.05 (-0.09, 0.2)	-0.14 (-0.38, 0.1)	-0.05 (-0.12, 0.02)

Species	**House Sparrow**	**Lesser Goldfinch**	**Mallard**	**Mourning Dove**	**Northern Flicker**	**Orange-crowned Warbler**
Intercept (Ψ)	-0.69 (-1.02, -0.36)	-2.34 (-2.86, -1.82)	-1.27 (-1.66, -0.88)	-1.22 (-1.66, -0.77)	1.42 (0.95, 1.89)	-0.79 (-1.22, -0.36)
Highly Developed	**0.65 (0.09, 1.21)**	-0.92 (-2.01, 0.18)	-0.37 (-1.09, 0.35)	**-1.18 (-2.12, -0.25)**	-0.34 (-1.07, 0.39)	0.01 (-0.71, 0.74)
Natural Areas	-0.27 (-0.99, 0.44)	-0.47 (-1.75, 0.81)	**1.15 (0.42, 1.87)**	0.68 (-0.18, 1.54)	**-0.94 (-1.81, -0.07)**	-0.2 (-1.15, 0.74)
Canopy Cover	**-0.32 (-0.61, -0.03)**	-0.25 (-0.76, 0.26)	-0.05 (-0.35, 0.26)	-0.22 (-0.59, 0.16)	0.21 (-0.18, 0.61)	-0.14 (-0.51, 0.23)
Detection (p)	-0.98 (-1.14, -0.82)	0.1 (-0.32, 0.51)	-1.43 (-1.73, -1.14)	-2.13 (-2.58, -1.68)	-1.65 (-1.78, -1.51)	-2.61 (-2.96, -2.27)
Day of Year	**-0.41 (-0.54, -0.27)**	**0.45 (0.18, 0.72)**	**-0.45 (-0.69, -0.21)**	**-0.98 (-1.23, -0.74)**	-0.02 (-0.14, 0.09)	**-0.7 (-0.99, -0.41)**
Day of Year^2	0.04 (-0.05, 0.12)	**-0.23 (-0.41, -0.06)**	0.02 (-0.13, 0.17)	0.12 (-0.03, 0.28)	**0.28 (0.21, 0.35)**	-0.11 (-0.3, 0.08)
Weekend	**0.25 (0.06, 0.45)**	0.04 (-0.34, 0.43)	0.12 (-0.21, 0.44)	0.3 (-0.06, 0.66)	0.04 (-0.11, 0.19)	-0.02 (-0.42, 0.37)
Time	0.02 (-0.08, 0.12)	0.05 (-0.15, 0.25)	**0.44 (0.24, 0.64)**	-0.17 (-0.38, 0.05)	**-0.24 (-0.32, -0.16)**	**-0.58 (-0.8, -0.37)**
Time^2	0.04 (-0.05, 0.14)	0.11 (-0.11, 0.32)	**-0.32 (-0.48, -0.15)**	**-0.25 (-0.45, -0.05)**	**0.12 (0.05, 0.2)**	0.19 (0, 0.38)
Temperature	**0.13 (0.02, 0.24)**	-0.06 (-0.26, 0.14)	0.04 (-0.17, 0.24)	**0.61 (0.44, 0.78)**	0.02 (-0.08, 0.12)	-0.01 (-0.26, 0.24)
Precipitation	-0.09 (-0.19, 0.01)	**-0.3 (-0.5, -0.11)**	0.11 (-0.04, 0.27)	-0.02 (-0.2, 0.17)	-0.06 (-0.13, 0.02)	-0.15 (-0.37, 0.06)
Mobility	**0.42 (0.3, 0.54)**	**-0.56 (-0.78, -0.34)**	**0.36 (0.19, 0.54)**	**0.64 (0.46, 0.81)**	**-0.3 (-0.39, -0.21)**	0.15 (-0.06, 0.35)
PM$_{2.5}$	**-0.12 (-0.22, -0.02)**	-0.1 (-0.3, 0.1)	**0.18 (0.03, 0.34)**	**-0.26 (-0.42, -0.09)**	**-0.1 (-0.17, -0.02)**	**-0.32 (-0.51, -0.12)**

Species	**Osprey**	**Pine Siskin**	**Purple Finch**	**Red-breasted Nuthatch**	**Red-winged Blackbird**	**Rock Pigeon**
Intercept (Ψ)	-1.7 (-2.19, -1.21)	-1.28 (-1.66, -0.91)	-1.88 (-2.38, -1.39)	-0.17 (-0.49, 0.16)	-1.7 (-2.11, -1.28)	-1.3 (-1.72, -0.88)
Highly Developed	-0.36 (-1.22, 0.5)	-0.74 (-1.51, 0.03)	-0.11 (-1.01, 0.79)	**-0.6 (-1.19, -0.01)**	**-0.93 (-1.8, -0.06)**	0.27 (-0.43, 0.97)
Natural Areas	0.83 (-0.14, 1.8)	-0.3 (-1.11, 0.51)	0.62 (-0.28, 1.51)	**-0.74 (-1.47, -0.01)**	**0.94 (0.21, 1.68)**	0.29 (-0.62, 1.2)
Canopy Cover	-0.35 (-0.78, 0.09)	0.17 (-0.14, 0.48)	0.21 (-0.16, 0.57)	**0.4 (0.13, 0.68)**	-0.16 (-0.49, 0.17)	-0.25 (-0.61, 0.11)
Detection (p)	-1.26 (-1.59, -0.92)	-0.65 (-0.87, -0.43)	-1.97 (-2.33, -1.61)	-0.99 (-1.15, -0.84)	-0.34 (-0.62, -0.06)	-1.7 (-1.96, -1.44)
Day of Year	0.09 (-0.24, 0.42)	**-0.62 (-0.81, -0.43)**	**-0.51 (-0.79, -0.24)**	0.02 (-0.11, 0.16)	**-0.66 (-0.86, -0.46)**	**0.4 (0.18, 0.62)**
Day of Year^2	-0.06 (-0.26, 0.15)	-0.12 (-0.24, 0)	-0.02 (-0.19, 0.15)	**0.11 (0.03, 0.19)**	-0.04 (-0.17, 0.1)	0.03 (-0.1, 0.17)
Weekend	0.19 (-0.24, 0.62)	-0.11 (-0.36, 0.15)	0.34 (-0.04, 0.72)	-0.07 (-0.25, 0.11)	0.23 (-0.08, 0.54)	0.12 (-0.19, 0.43)
Time	**1.41 (1.04, 1.78)**	0.13 (0, 0.25)	**-0.37 (-0.57, -0.16)**	-0.07 (-0.16, 0.02)	**0.55 (0.39, 0.72)**	-0.07 (-0.24, 0.09)
Time^2	**-1.02 (-1.28, -0.77)**	**-0.17 (-0.29, -0.05)**	**0.2 (0.03, 0.38)**	-0.02 (-0.11, 0.07)	**-0.54 (-0.7, -0.37)**	**-0.19 (-0.35, -0.04)**
Temperature	**0.47 (0.18, 0.77)**	**0.29 (0.14, 0.45)**	0.01 (-0.21, 0.24)	0 (-0.11, 0.11)	**0.34 (0.18, 0.5)**	0.06 (-0.11, 0.23)
Precipitation	-0.01 (-0.24, 0.21)	0.03 (-0.08, 0.14)	-0.02 (-0.2, 0.15)	**0.1 (0.02, 0.18)**	0.1 (-0.05, 0.25)	-0.14 (-0.31, 0.03)
Mobility	**-0.38 (-0.62, -0.14)**	**0.4 (0.28, 0.52)**	**0.62 (0.44, 0.79)**	**0.2 (0.11, 0.29)**	**0.32 (0.18, 0.46)**	**-0.32 (-0.53, -0.12)**
$PM_{2.5}$	-0.22 (-0.48, 0.04)	-0.01 (-0.13, 0.12)	0.05 (-0.13, 0.23)	0.02 (-0.07, 0.12)	0.04 (-0.11, 0.19)	-0.03 (-0.2, 0.13)

Species	**Ruby-crowned Kinglet**	**Rufous Hummingbird**	**Song Sparrow**	**Spotted Towhee**	**Steller's Jay**	**Tree Swallow**
Intercept (Ψ)	-0.79 (-1.26, -0.31)	-0.66 (-1.08, -0.25)	0.66 (0.32, 0.99)	0.66 (0.32, 1)	1.16 (0.74, 1.58)	-1.48 (-1.96, -1)
Highly Developed	-0.48 (-1.31, 0.35)	**-0.96 (-1.77, -0.16)**	**-0.57 (-1.12, -0.02)**	**-0.6 (-1.17, -0.04)**	-0.29 (-0.98, 0.41)	-0.06 (-0.88, 0.75)
Natural Areas	-0.04 (-1.13, 1.05)	0.65 (-0.19, 1.5)	-0.6 (-1.26, 0.07)	-0.37 (-1.07, 0.33)	**-0.98 (-1.77, -0.18)**	**1.02 (0.13, 1.92)**
Canopy Cover	0.12 (-0.28, 0.52)	-0.23 (-0.57, 0.12)	**0.33 (0.05, 0.6)**	**0.39 (0.09, 0.69)**	0.26 (-0.09, 0.62)	-0.3 (-0.7, 0.09)
Detection (p)	-7.28 (-9.03, -5.53)	-2.17 (-2.47, -1.86)	-0.58 (-0.7, -0.46)	-0.54 (-0.67, -0.42)	-1.33 (-1.47, -1.19)	-1.95 (-2.28, -1.61)
Day of Year	**-8.24 (-11.27, -5.22)**	**0.26 (0.01, 0.51)**	-0.06 (-0.17, 0.04)	-0.1 (-0.21, 0.01)	0.1 (-0.03, 0.22)	-0.24 (-0.52, 0.03)
Day of Year^2	**-2.65 (-3.97, -1.34)**	-0.15 (-0.32, 0.01)	**0.1 (0.03, 0.16)**	-0.07 (-0.14, 0)	0.07 (-0.01, 0.14)	-0.05 (-0.23, 0.13)
Weekend	**-0.66 (-1.16, -0.15)**	-0.08 (-0.44, 0.29)	0.07 (-0.08, 0.22)	-0.04 (-0.19, 0.11)	0.04 (-0.13, 0.2)	0 (-0.4, 0.41)
Time	**-0.4 (-0.66, -0.14)**	0.03 (-0.16, 0.22)	**-0.23 (-0.3, -0.15)**	**-0.3 (-0.38, -0.23)**	**-0.2 (-0.29, -0.12)**	**0.26 (0.03, 0.49)**
Time^2	-0.08 (-0.34, 0.19)	0.02 (-0.15, 0.19)	0.05 (-0.02, 0.11)	**0.1 (0.03, 0.17)**	**-0.09 (-0.18, -0.01)**	**-0.29 (-0.49, -0.1)**
Temperature	0 (-0.38, 0.38)	**-0.24 (-0.44, -0.03)**	-0.04 (-0.13, 0.05)	-0.08 (-0.17, 0.02)	**-0.16 (-0.27, -0.06)**	0.17 (-0.05, 0.39)
Precipitation	0.05 (-0.19, 0.3)	0 (-0.17, 0.17)	0.06 (-0.01, 0.13)	0.02 (-0.05, 0.09)	**0.08 (0.01, 0.16)**	0.01 (-0.19, 0.21)
Mobility	-0.39 (-0.78, 0)	**0.38 (0.23, 0.53)**	**0.11 (0.04, 0.18)**	**0.33 (0.25, 0.4)**	0 (-0.09, 0.09)	**0.78 (0.59, 0.97)**
$PM_{2.5}$	-0.04 (-0.23, 0.15)	0.15 (-0.03, 0.34)	-0.05 (-0.12, 0.02)	0.01 (-0.07, 0.08)	0.03 (-0.06, 0.11)	-0.05 (-0.26, 0.15)

Species	**Violet-green Swallow**	**White-crowned Sparrow**	**Wilson's Warbler**	**Yellow-rumped Warbler**	**Violet-green Swallow**	**White-crowned Sparrow**
Intercept (Ψ)	-1.31 (-1.71, -0.92)	-0.88 (-1.24, -0.51)	-0.67 (-1.08, -0.26)	-0.52 (-0.95, -0.1)	-1.31 (-1.71, -0.92)	-0.88 (-1.24, -0.51)
Highly Developed	-0.44 (-1.19, 0.31)	0.1 (-0.51, 0.71)	0.44 (-0.27, 1.14)	-0.3 (-1.01, 0.4)	-0.44 (-1.19, 0.31)	0.1 (-0.51, 0.71)
Natural Areas	0.45 (-0.3, 1.2)	**0.79 (0.04, 1.54)**	-0.45 (-1.37, 0.46)	-0.04 (-0.97, 0.9)	0.45 (-0.3, 1.2)	**0.79 (0.04, 1.54)**
Canopy Cover	0.1 (-0.21, 0.41)	**-0.4 (-0.71, -0.08)**	0.27 (-0.07, 0.61)	-0.22 (-0.57, 0.13)	0.1 (-0.21, 0.41)	**-0.4 (-0.71, -0.08)**
Detection (p)	-1.11 (-1.37, -0.86)	-1.4 (-1.61, -1.19)	-1.88 (-2.16, -1.6)	-4.36 (-5.07, -3.65)	-1.11 (-1.37, -0.86)	-1.4 (-1.61, -1.19)
Day of Year	**-0.37 (-0.58, -0.16)**	**-0.51 (-0.67, -0.35)**	**-0.62 (-0.89, -0.34)**	**-6.25 (-7.77, -4.73)**	**-0.37 (-0.58, -0.16)**	**-0.51 (-0.67, -0.35)**
Day of Year^2	**-0.29 (-0.43, -0.15)**	**0.17 (0.06, 0.28)**	**-1.03 (-1.27, -0.8)**	**-3.48 (-4.33, -2.63)**	**-0.29 (-0.43, -0.15)**	**0.17 (0.06, 0.28)**
Weekend	-0.18 (-0.49, 0.14)	0.09 (-0.14, 0.33)	**0.4 (0.07, 0.74)**	-0.37 (-0.76, 0.01)	-0.18 (-0.49, 0.14)	0.09 (-0.14, 0.33)
Time	0.07 (-0.08, 0.22)	**-0.24 (-0.37, -0.1)**	-0.09 (-0.25, 0.08)	-0.03 (-0.24, 0.19)	0.07 (-0.08, 0.22)	**-0.24 (-0.37, -0.1)**
Time^2	0.04 (-0.09, 0.18)	**-0.26 (-0.39, -0.14)**	**0.19 (0.04, 0.34)**	0.17 (-0.02, 0.36)	0.04 (-0.09, 0.18)	**-0.26 (-0.39, -0.14)**
Temperature	-0.1 (-0.29, 0.08)	0.05 (-0.08, 0.18)	-0.19 (-0.4, 0.03)	-0.22 (-0.52, 0.08)	-0.1 (-0.29, 0.08)	0.05 (-0.08, 0.18)
Precipitation	-0.11 (-0.26, 0.04)	0.07 (-0.05, 0.19)	-0.16 (-0.33, 0.01)	-0.14 (-0.34, 0.05)	-0.11 (-0.26, 0.04)	0.07 (-0.05, 0.19)
Mobility	**0.77 (0.64, 0.91)**	**0.3 (0.19, 0.41)**	**0.62 (0.42, 0.83)**	**-0.5 (-0.76, -0.25)**	**0.77 (0.64, 0.91)**	**0.3 (0.19, 0.41)**
PM$_{2.5}$	**0.22 (0.06, 0.37)**	-0.06 (-0.18, 0.05)	-0.09 (-0.28, 0.11)	-0.06 (-0.25, 0.12)	**0.22 (0.06, 0.37)**	-0.06 (-0.18, 0.05)

VITA

Ms. Olivia Sanderfoot is a graduate researcher in the Quantitative Ecology Lab at the University of Washington School of Environmental and Forest Sciences. In her research, Ms. Sanderfoot uses community science data and field measurements to study how urban air pollution and wildfire smoke impact birds and other wildlife. In addition to her doctoral studies, Ms. Sanderfoot holds two degrees from the University of Wisconsin–Madison, including a Bachelor of Science in biology, Spanish, and environmental studies and a master's degree in environmental science. Ms. Sanderfoot is driven by her passion for environmental policy and conservation, her love for birds, and her strong belief in the Wisconsin Idea, the philosophy that a university's research should be applied to solve problems and improve the health, well-being, and environment of the community it serves. Ms. Sanderfoot has been interviewed about her research by *National Geographic*, *Discover Magazine*, *Audubon Magazine*, *Popular Science*, *The Seattle Times*, *The Washington Post*, *Crosscut*, *Inside Climate News*, and several local radio stations. Her letters to the editor and op-eds appear in *The New York Times* and *The Spokesman-Review*. Ms. Sanderfoot received the National Science Foundation Graduate Research Fellowship in 2016 and an honorable mention in the Ford Foundation Predoctoral Competition in 2018. In 2020, she was named one of the Husky 100 by the University of Washington. This award is one of the university's top honors, recognizing students for their discovery mindset, capacity for leadership, and commitment to inclusive community.