A bird's-eye view of air pollution

The impacts of health-damaging air pollutants on avifauna

by

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Abstract

Despite the well-established links between air pollution and human health, vegetation, and aquatic ecosystems, less attention has been paid to the potential impact of reactive atmospheric gases and aerosols on avian species. In this thesis, I synthesize and analyze findings published since 1950 regarding avian responses to air pollution and discuss knowledge gaps that could be addressed in future studies. I find consistent evidence for adverse health impacts on birds attributable to exposure to gas-phase and particulate air pollutants, including carbon monoxide (CO), ozone (O₃), sulfur dioxide (SO₂), smoke, and heavy metals, as well as mixtures of urban and industrial emissions. Avian responses to air pollution include respiratory distress and illness, impaired reproductive success, increased detoxification effort, elevated stress levels, immunosuppression, and behavioral changes. Exposure to air pollution may furthermore reduce population density, species diversity, and species richness in bird communities. This thesis constitutes a key step in determining if the secondary National Ambient Air Quality Standards (NAAQS) set by the United States Environmental Protection Agency (EPA) to protect public welfare are sufficient in safeguarding avifauna from the adverse health outcomes associated with air pollution. To my knowledge, this is the first meta-analysis of studies examining the effects of reactive gases and aerosols on non-human species.
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I. Introduction

Birds are a valued component of public welfare for myriad reasons. Birds play an integral role in ecosystems around the world, acting as keystone predators, foragers, and scavengers. There are over 10,000 species of birds; together they represent an incredible reservoir of genetic diversity that supports nature’s grand resiliency. Studying birds provides scientists with the opportunity to learn more about life history strategies, physiological mechanisms, and the evolution of flight. The mere existence of birds is of benefit to mankind, as these animals are of great cultural significance to societies around the world, and their charisma is frequently exploited by conservation groups to create more engaging educational programming.

It is clear that birds are negatively impacted by many of the environmental challenges we face today, including urbanization, habitat degradation, and climate change. Air pollution may also impose undue stress on birds, resulting in long-term, negative effects on fitness and possibly leading to demographic consequences, such as reduced population size or density or shifts in community composition. Unfortunately, research on the topic of avian responses to air pollution is limited at best.

It is possible that disciplinary divides may be inhibiting the research community from learning more about how birds are affected by air quality. It became evident in developing this thesis that there has been little collaboration amongst atmospheric chemists, ecologists, toxicologists, ornithologists, and veterinarians on characterizing avian responses to air pollution. To my knowledge, this thesis is the only work to date...
with the goal of linking research on this topic from distinct fields. In this thesis, I synthesize and analyze findings from numerous fields of study on avian responses to air pollution to support future research on this important topic and inform public policy. To provide context for this work, this chapter presents key background information on air pollution, air quality regulation, avian respiration, and the cultural significance of birds.

**Our Atmosphere**

This thesis explores avian responses to air pollution, so it is useful to begin by considering the nature of air pollution as an environmental problem. Planet Earth is encompassed by a blanket of gases we refer to as our *atmosphere*. Though thin relative to our planet's radius, our atmosphere is essential in supporting life on Earth by insulating Earth's surface from the sun's harmful ultraviolet rays. Our atmosphere also plays a key role in the hydrologic cycle and the cycling of nutrients, including carbon, nitrogen, and phosphorus. Our atmosphere is made up almost entirely of nitrogen (78%), oxygen (21%), and argon (0.9%) in proportions that do not vary spatially or temporally. Trace gases and aerosols account for just one-tenth of the atmosphere's chemical composition, yet the concentrations of these compounds, constantly in flux, dramatically affect both air quality and the capacity of our atmosphere to retain heat.

Both human activity and natural processes contribute to the concentrations of trace gases and aerosols in our atmosphere, sometimes referred to as pollutants.
Primary air pollutants are gases and aerosols that are directly emitted to the atmosphere. Secondary air pollutants are gases and aerosols that are formed in the atmosphere due to complex chemical reactions. Though vastly outnumbered by the mixing ratios of nitrogen, oxygen, and argon, the ambient concentrations of primary and secondary air pollutants, whether of natural or anthropogenic origin, determine the quality of the air we breathe and the degree of global warming that occurs within our atmosphere.

Air Pollution & Human Health

There are thousands of different trace gases and aerosols found in the atmosphere, each with a unique chemical composition and set of properties. While some air pollutants are highly reactive, others are inert. The chemical lifetime of air pollutants is therefore highly variable. For example, the characteristic oxidation time for benzene (C₆H₆), a volatile organic compound, is 9.6 days, while the characteristic oxidation time for methane (CH₄), a greenhouse gas, is 4.1 years.¹ Long-lived greenhouse gases, including methane, carbon dioxide (CO₂), and nitrous oxide (N₂O), contribute to global warming by trapping the heat of infrared radiation emitted by Earth’s surface. Reactive gases and aerosols, including volatile organic compounds (VOCs), nitrogen dioxide (NO₂), and ozone (O₃), are less of a concern when considering

the capacity of the atmosphere to retain heat because these compounds are rapidly consumed in chemical reactions or deposited to Earth’s surface.

However, reactive gases and aerosols are often associated with adverse human health impacts. For example, exposure to O₃ and particulate matter (PM, referring to any solid or liquid suspended in the air) has been linked to cardiovascular disease, respiratory disease, and premature mortality. In fact, exposure to health-damaging air pollutants such as PM and O₃ is a leading contributor to the global burden of disease and leads to millions of premature deaths each year, according to research conducted by the Institute for Health Metrics and Evaluation (IHME). IHME ranked exposure to ambient PM as the 5th leading risk factor for mortality worldwide. Household air pollution is ranked 10th and exposure to ambient O₃ is ranked 33rd. Exposure to air pollution is clearly detrimental to human health.

Air Quality Regulation

While there are natural sources of reactive gases and aerosols, high outdoor concentrations of health-damaging air pollutants are primarily driven by human activity. Environmental regulation designed to control both emissions of air pollutants and ambient concentrations of specific compounds is effective in reducing human exposure to health-damaging air pollutants. In the United States, the Environmental Protection Agency (EPA) is granted the authority to regulate air quality to protect

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public health and the environment under the Clean Air Act. According to a report issued by the Office of Management & Budget (OMB) in 2014, the estimated benefits of regulations imposed by the EPA’s Office of Air & Radiation amount to three times the costs of their implementation. In fact, the OMB estimated that 98% to 99% of all the benefits of environmental policy set by the EPA are associated with rules designed to improve air quality. While expensive, air quality regulation is evidently a worthwhile investment.

The National Ambient Air Quality Standards (NAAQS) set by the EPA are a key component of the regulatory framework established to reduce air pollution and improve air quality in the United States. Primary NAAQS are designed to protect public health by limiting ambient concentrations of health-damaging air pollutants that have been linked to cardiovascular and respiratory disease. Secondary NAAQS are intended to protect public welfare by improving visibility and reducing damage to infrastructure, vegetation, crops, and animals, including birds. Given the limited number of studies regarding the impacts of air pollution on wildlife, it is unclear if the secondary NAAQS are sufficient to protect our nation’s rich biodiversity. Research does show that air pollution negatively impacts ecosystems. Ozone damages the leaf tissue of plants and industrial and agricultural emissions lead to the deposition of sulfuric and nitric acids to lakes and rivers, commonly referred to as “acid rain.” This adversely impacts fisheries and the wildlife dependent on freshwater habitat. Additional research is needed to determine if current air quality regulation is sufficient to protect wildlife

from elevated ambient concentrations of health-damaging air pollutants. Birds in particular are likely more susceptible to the negative health effects associated with air pollution because they respire more efficiently than any other type of terrestrial vertebrate. This thesis focuses on identifying known avian responses to air pollutants regulated by the EPA to determine if the secondary NAAQS set by the EPA should be additionally stringent to protect the hundreds of bird species living in the United States and provide additional policy recommendations to protect birds as a vital component of public welfare.

The Cultural Significance of Birds

There are well over 10,000 species of birds on Planet Earth. They persist on every continent, occupy myriad habitats, and serve as living, breathing examples of evolution in action, demonstrating the intimate tie between form and function that drives natural selection. Humans have always been fascinated by these feathered descendants of dinosaurs. Over thousands of years, birds have become an important cultural symbol. In the U.S., for example, the American Robin is often considered a harbinger of spring while in rural areas of southern Africa vultures are often said to be a sign of impending doom.

Across many cultures, birds have also come to symbolize human vulnerability to environmental change. In the early 1900s, coal miners brought canaries down into the mines to help monitor levels of noxious gases, leading to the use of the colloquial phrase
“canary in the coal mine” to refer to an early-warning signal of some future danger. In the 1960s, Rachel Carson’s award-winning book *Silent Spring* brought attention to the widespread impact of pesticide and insecticide applications on wildlife, especially songbirds, a message that struck a chord with hundreds of thousands of people and inspired the movement that led to the establishment of the EPA. Today, birds have been assessed for their value in the biomonitoring of heavy metals and persistent organic pollutants, and work by citizen scientists shows that birds are responding to the warmer temperatures brought about by climate change.

Despite the demonstrated importance of birds to society, several knowledge gaps remain in the scientific community’s understanding of how human activity affects these animals. Research clearly shows that birds are negatively impacted by land use change, urbanization, habitat fragmentation, and contamination of freshwater and saltwater habitats, but substantially less is known about how air quality affects wild avian populations. There is no doubt that respiratory exposure to health-damaging air pollutants poses a risk to humans, and birds respire more efficiently than we do. This likely renders birds more susceptible to the adverse health impacts associated with air pollution. However, studies on how birds respond to air pollution are few in number, and until now have not been compiled in a meaningful way. This has made it difficult to pinpoint species-specific responses at the physiological and demographic level. Ecologists and atmospheric chemists should work together to extend the vast literature on air pollution and human health to consider how air quality affects birds, animals that
are not only vitally important to dozens of ecosystems but also have great cultural significance in communities around the world.

**Avian Respiration**

Birds respire much more efficiently than mammals, thanks to the unique structure of the avian respiratory system. Avian lungs do not expand and contract like those of mammals. Instead, birds utilize a series of air sacs — thin-walled structures that act as bellows — to constantly push fresh air into their lungs. This strategy supports unidirectional air flow, maximizing contact of fresh, oxygenated air with the gas exchange surfaces of the lungs. Gas exchange is the primary purpose of respiration. The respiratory system supplies the body with oxygen (O\textsubscript{2}) and removes CO\textsubscript{2}, a waste product of metabolic activity.

Because avian lungs do not expand and contract like those of mammals, birds manipulate their skeletal structure to alter the pressure in the respiratory system as needed to draw and expel air. To do so, birds lower the sternum in inhalation and raise the sternum in exhalation. Lowering the sternum during inhalation expands the ribcage, opening up the chest cavity and extending the air sacs. This reduces the pressure within the air sacs, which then pull in air. Raising the sternum contracts the ribcage, compressing the chest cavity and the air sacs. This increases the pressure within the air sacs, which then expel air. These movements are synchronized with wingbeats when birds are in flight.
Avian respiration occurs in four steps, or two cycles of inspiration and expiration, as described below:

- **Step #1 (Inhalation):** Air is inhaled through the nostrils at the base of the beak and pulled down the trachea, through the primary bronchi, to the posterior air sacs.

- **Step #2 (Exhalation):** Air held in the posterior air sacs is pushed through the secondary and tertiary bronchi to tiny air capillaries in the lung. The air capillaries crisscross blood capillaries, allowing gas exchange to occur. The blood capillaries take up O₂ as the air capillaries take up CO₂.

- **Step #3 (Inhalation):** O₂-depleted air is pulled from the lung into the anterior air sacs.

- **Step #4 (Exhalation):** O₂-depleted air held in the anterior air sacs is pushed through the primary bronchi, up the trachea, and out of the nostrils.

These four steps track how air moves through the avian respiratory system. In reality, air flow is constant, and the steps that occur during inhalation (#1 and #3) or exhalation (#2 and #4) transpire simultaneously. As the ribcage expands, inhalation pulls air from the environment into the respiratory system to be held in the posterior air sacs while O₂-depleted air is pulled from the lung into the anterior air sacs. As the ribcage contracts, air is expelled from the air sacs, causing O₂-rich air held in the posterior air sacs to flow into the lung and CO₂-rich air held in the anterior air sacs to exit the body. Unlike in mammals, air enters the lung during expiration and exits the lung during inspiration. The unidirectional flow of air replaces nearly all the air contained in the lungs with each breath. This helps maximize the efficiency of gas exchange. In addition to supporting unidirectional air flow, the air sacs also help to reduce the heat generated by birds in flight and protect their internal organs.
Another important characteristic of the avian respiratory system is crosscurrent gas exchange, a strategy that further improves the efficiency of avian respiration. Crosscurrent gas exchange occurs when air capillaries and blood capillaries are positioned at right angles. This greatly increases the diffusion of $O_2$ from the air to the blood.

The unique structure of the avian respiratory system enables birds to move a greater volume of oxygenated air through their lungs with each breath as compared to mammals, and crosscurrent gas exchange between the air and blood capillaries in the lungs provides for even more efficient respiration. This allows birds to sustain flight in environments that could be life-threatening to mammals, such as the high altitudes of the Himalayan mountain range through which the Bar-headed Goose migrates each year. Given the efficiency of the avian respiratory system and the high ventilation rates required during flight, it is reasonable to expect that birds might also be more susceptible to the negative health effects associated with respiratory exposure to reactive gases and aerosols.

An Original Meta-analysis

In this thesis, I conduct a meta-analysis of research findings on avian responses to air pollution spanning a multitude of disciplines. In chapter two, I synthesize and analyze findings published since 1950 on avian responses to reactive gases and aerosols and discuss knowledge gaps that could be addressed in future studies. Please
note that this chapter constitutes work in review at *Environmental Research Letters*. *Environmental Research Letters* is one of the leading interdisciplinary journals in the environmental sciences, and review articles must follow a quantitative methodology that draws from the medical review literature. According to the publisher, review articles are “systematic, evidence-based reviews of important and topical environmental issues… The journal hopes to lead the way in publishing more quantitative, meta-data based reviews of important environmental questions.” In the final chapter of this thesis, I consider the implications of this meta-analysis for air quality policy and propose several ideas for future studies on this important research topic.
II. A review of air pollution impacts on avian species

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I. Introduction:

It is well established in the peer-reviewed literature that exposure to air pollution causes adverse human health outcomes, including increased risk of respiratory disease, cardiovascular disease, cancer, and mortality [West et al., 2016, and references therein]. Public health research dating back to the 1950s has established linkages between these adverse health outcomes and respiratory exposure to ambient air pollutants, including tropospheric ozone (O₃), aerosols (or particulate matter, PM), nitrogen dioxide (NO₂), sulfur dioxide (SO₂), carbon monoxide (CO), heavy metals (e.g. lead, mercury), certain hydrocarbons, and other chemically and biologically active species present in the air. Beyond human health, research suggests that all ecosystem types are vulnerable to the effects of air pollution [Lovett et al., 2009], with most work to date focused on characterizing the impacts of air pollution on vegetation and aquatic environments. Ozone, in particular, has been shown to reduce rates of photosynthesis in plants [Reich and Amundson, 1985], and the acidification of lakes resulting from SO₂ and NOₓ (NO₂ + NO) emissions affects both species diversity and species richness in
freshwater communities [Brönmark and Hansson, 2002].

To date few studies have explored how chemical characteristics of the air affect non-human animal species, especially in wild populations. In fact, searching the Thomson Reuters Web of Science platform in November 2016 (referred to hereafter as WoS) for articles related to “‘air pollution’ and ‘human health’” published since 1950 produced 2,388 results, while searching for articles related to “‘air pollution’ and ‘animals’” or “‘air pollution’ and ‘wild populations’” produced 658 and 3 results, respectively.

Among non-human animal species, birds may be particularly vulnerable to health-damaging air pollutants. The avian respiratory system, unlike the mammalian respiratory system, is characterized by unidirectional airflow, a thin blood-gas barrier, and cross-current gas exchange, all features that improve the efficiency of respiration. In fact, birds respire more efficiently than any other type of terrestrial vertebrate. Avian species are therefore more likely to be susceptible to high concentrations of reactive gases and aerosols in the air than mammalian species, and so may serve as useful indicators of air quality [Brown et al., 1997]. The literature on this topic is limited: a WoS search for articles related to “‘air pollution’ and ‘birds’” and “‘air quality’ and ‘birds’” produced just 132 and 87 results, respectively. Of the articles found in the latter search, the top three were focused on the effects of poor air quality on poultry, not on wild bird populations.

Birds have long been recognized as sentinel species for environmental change. In the early 20th century, caged canaries were brought down into coal mines to signal
when carbon monoxide and methane concentrations in the mines reached unsafe levels, a practice which led to the use of the colloquial phrase “canary in the coal mine” to refer to early warning signs of future danger. Rachel Carson’s award-winning book *Silent Spring*, published in 1962, brought attention to the widespread impact of pesticide and insecticide applications on songbirds. A number of avian species have been assessed for their value in the biomonitoring of heavy metals [Burger and Gochfeld, 1995, 1997; Saldiva and Böhm, 1998; Dauwe et al., 2003; Manjula et al., 2015] as well as polychlorinated biphenyls and other organic contaminants [Arenal et al., 2004; Miniero et al., 2008]. Chronic dietary exposure to heavy metals — including aluminum, cadmium, mercury, and lead — has been shown to limit avian reproductive success [Scheuhammer, 1987], and dietary exposure to dichlorodiphenyltrichloroethane (DDT) — a chemical commonly used in pesticides and insecticides in the mid-20th century — appears to affect calcium metabolism in avian species [Jefferies, 1969] and leads to death in songbirds [Wurster et al., 1965; Hill et al., 1971]. Ecologists have also identified a number of responses to climate change in wild bird populations, including phenological shifts in the timing of spring migration and altered species composition of overwintering bird communities [Jones et al., 2012; Princé and Zuckerberg, 2015]. A WoS search for articles related to “climate change’ and ‘birds’” found 3,507 results, with the top paper cited nearly 3,800 times.

Birds could also serve as sentinel species for air quality, as they are found globally, in both urban and rural areas, and make use of many different habitat types [Brown et al., 1997; Baesse et al., 2015]. Their wide flight ranges could be beneficial in
studying and understanding the spatial distribution of air pollutants [Saldiva and Böhm, 1998]. Here we present a summary of findings regarding avian responses to air pollution, with an emphasis on inhalation exposure. Our focus on the respiratory system is motivated by the high metabolic rates of birds and expansive literature on human health outcomes associated with inhalation exposure to air pollutants. Below we outline study methods, discuss key findings, and highlight the role of future research. Key findings are divided into six sections: 1) respiratory distress and illness, 2) impaired reproductive success, 3) increased detoxification effort, elevated stress levels, and immunosuppression, 4) behavioral changes, 5) habitat degradation, and 6) demographic responses. We aim to provide foundational knowledge on avian responses to air pollution, and to support a broader research effort on air pollution impacts on birds.

II. Methods:

An initial literature review was performed in January 2016 to gather peer-reviewed studies on avian responses to reactive gases and aerosols. This literature review was performed again in November 2016 to capture more recent publications. Searches were conducted using Thomson Reuters Web of Science platform, accessed through the University of Wisconsin library system. Key search terms included:
Each term was paired with the words “birds” and “avian” in various combinations, utilizing both the “title” and “topic” fields in the basic search function. Over 200 searches were performed. Search results were refined so that only articles or reviews published in English since 1950 were included in the lists of articles generated by Web of Science. Additional references cited in these studies or citing these studies were also considered. Studies examining poultry-keeping systems were excluded, as these studies did not provide insight into how exposure to outdoor air pollution may affect wild birds. However, laboratory studies designed to investigate the effects of inhalation exposure to ambient air pollutants in birds were included, although some of these studies did use domesticated species, such as chickens, as study specimens.

III. Key Findings:

To date, three general approaches have been used to characterize avian responses to respiratory exposure to air pollution. Researchers have exposed birds to
gaseous mixtures or specific concentrations of gases or aerosols in laboratory experiments, an approach which we refer to as “controlled exposure.” Birds have also been monitored in natural habitats or caught in the wild for further study, capturing in situ exposure. Finally, we include case studies relevant to avian sensitivity to air pollution. We report key findings below and note which of these three general approaches (controlled exposure, in situ exposure, or case study) was used to elucidate these findings.

III.1 Respiratory distress and illness

Studies have shown that both controlled and in situ exposure to air pollutants cause morphological and physiological changes in the avian respiratory system. Exposure to air pollution clearly causes respiratory distress in birds and increases their susceptibility to respiratory infection.

A. Controlled exposure

Birds, like other vertebrate species, are susceptible to carbon monoxide poisoning. Carbon monoxide (CO) is a product resulting from the incomplete combustion of fossil fuels and biomass. Exposure to CO results in the formation of carboxyhemoglobin (HbCO), limiting the capacity of hemoglobin to transport oxygen to tissues throughout the body [Baker and Tumasonis, 1972]. Treatment for carbon monoxide poisoning in birds typically includes provision of supplemental oxygen,
which reduces the half-life of HbCO [Verstappen and Dorrestein, 2005; Simone-Freilicher, 2008]. The avian carbon monoxide poisoning mechanism was explored in a 1974 study [Tschorn and Fedde, 1974], which suggested that CO may depress inhibitory interneurons in the central nervous system, resulting in the abnormal breathing associated with CO poisoning observed in the study specimens.

Ozone (O$_3$) also appears to pose a health risk to birds by causing morphological and physiological changes in the avian respiratory system [Rombout et al., 1991; Cuesta et al., 2005]. Ozone in near-surface environments is chemically formed through reactions involving nitrogen oxides (NO$_x$) and volatile organic compounds (VOCs) in the presence of sunlight. In a study by Rombout et al. [1991], adult, male Japanese quail (Coturnix coturnix japonica) were exposed to varying O$_3$ concentrations, and exposure to 0.50 parts per million (ppm) O$_3$ resulted in the reduction and shortening of cilia in the trachea and bronchi (Figure 1), hypertrophy in the secondary bronchi, hemorrhaging and inflammation in the capillary network, necrosis of epithelial cells lining the air capillaries, and symptoms of pulmonary edema. Quail exposed to higher concentrations of O$_3$ (1.50 ppm) were more severely affected. Individuals in this treatment group showed a dramatic reduction in the number of ciliated cells in the trachea and bronchi. Hemorrhaging and changes in the structure of the atrial epithelium resulted in the closing of the atrial space, reducing air flow and possibly contributing to the labored breathing exhibited by this treatment group during the experiment. Only the birds in this treatment group presented a statistically significant increase in lung weight and lactate dehydrogenase (LDH) activity [Rombout et al.,
1991, often considered a response to injury or stress. Cuesta et al. [2005] also found a statistically significant increase in expression of adrenomedullin-like protein between pigeons (Columba livia domestica) exposed to high levels of O₃ and a control group, which appears to be the only study to date on air pollution impacts on adrenomedullin-like immunoreactivity in birds, a sign of respiratory distress.

![Image](image_url)

**Figure 1:** Standard electron microscopy (2000x) of the epithelium of a secondary bronchus in a) a Japanese quail exposed to 0.0 ppm O₃ and b) a Japanese quail exposed to 0.50 ppm O₃. Note the reduction and shortening of cilia in the individual exposed to O₃. Imagery from Rombout et al., 1991.

Exposure to sulfur dioxide (SO₂) may impair the avian immune response to inhaled antigens, making birds more susceptible to disease [Wakabayashi et al., 1977]. Sulfur dioxide is a gas that is emitted from the combustion of sulfur-containing fuels, such as coal or petroleum oil. Results from a 1977 study show that exposure to SO₂, even at concentrations as low as 1.4 ppm, compromises the effectiveness of the mucociliary system in White Leghorn chickens, which plays a crucial role in reducing
the incidence of respiratory disease by clearing contaminants, including infectious agents, from the airway [Wakabayashi et al., 1977]. Fedde and Kuhlmann [1979] found that White Leghorn chickens exposed to much higher concentrations of SO$_2$ (>1,000 ppm) exhibited signs of respiratory distress, and the majority of those exposed to SO$_2$ at a concentration of 5,000 ppm died.

Multiple studies have shown that birds are also likely affected by elevated concentrations of particle pollution [Sterner, 1993a, 1993b; Tell et al., 2006; Tell et al., 2012]. Particulate matter (PM) includes any liquid or solid suspended in the air, typically classified by size such that PM$_{2.5}$ represents PM less than 2.5 microns in diameter and PM$_{10}$ represents PM less than 10 microns in diameter. Health-relevant PM can include directly emitted particles, such as wind-blown dust or smoke from fires, and/or chemically formed particles, such as sulfate and nitrate aerosols. Tell et al. [2006] examined the use of an aerosolized fluorescent microsphere technique of their own design to study particle deposition in adult domestic pigeons. Their results demonstrated that smaller particles (those less than three microns in diameter) are more likely to be well dispersed in the avian respiratory system than larger particles (those greater than six microns in diameter), which are more likely to remain in the upper airway [Tell et al., 2006]. Tell et al. [2012] confirmed that the extent of deposition increases with exposure time [Tell et al., 2012]. Understanding how particles are deposited in the respiratory system and cleared from the airway will be important in differentiating responses to acute and chronic exposure to air pollution.
B. *In situ* exposure

A number of studies have used microscopic imagery and chemical analysis to compare the morphology and biochemistry of lung tissue from birds captured in urban and rural areas in order to discern physiological differences that are likely attributable to urban air pollution [Lorz and López, 1997; Cuesta et al., 2005; Sicolo et al., 2009, Ejaz et al., 2014; Steyn and Maina, 2015]. Birds exposed to urban air pollution may exhibit a buildup of cellular and mineral debris leading to lung parenchymal consolidation or alveolar consolidation, a characteristic condition of pneumonia [Ejaz et al., 2014]. Researchers in Spain have showed that urban air pollution may also impact the avian pulmonary surfactant system [Lorz and López, 1997; Cuesta et al., 2005].

Pulmonary surfactant is a lipoprotein complex, and the secretion of pulmonary surfactant helps reduce tension in the respiratory system, thus preventing the lungs from collapsing during expiration [Lorz and López, 1997; Cuesta et al., 2005]. Pulmonary surfactant also plays an important role in the defense mechanisms of the lung. The lipids and proteins that make up the surfactant are stored in lamellar bodies — dense structures found in the cytoplasm of type II pneumocytes [Lorz and López, 1997]. In a 1997 study, pigeons were captured and studied to determine if the number of lamellar bodies in lung tissue differed between birds living in rural habitats (collected from a farm in the village of Guadalajara) and urban habitats (captured in the city of Madrid). If more pulmonary surfactant is excreted by type II pneumocytes, the number of lamellar bodies would be expected to decline. The researchers found a 33% reduction in the quantity of lamellar bodies in urban birds as compared to rural birds,
indicative of elevated secretion of pulmonary surfactant and, therefore, respiratory
distress [Lorz and López, 1997].

Phosphatidylcholine is an important component of pulmonary surfactant. In
mammals, secretion of phosphatidylcholine is stimulated by adrenomedullin, a peptide
hormone. Elevated concentrations of adrenomedullin have been documented in the
pathologies for several mammalian respiratory diseases, including asthma. A 2005
study demonstrated the presence of an adrenomedullin-like protein in the avian
respiratory system [Cuesta et al., 2005]. In this study, pigeons were captured and
observed to determine if expression of this adrenomedullin-like protein differed
between birds living in rural and urban habitats. Results showed that expression of the
adrenomedullin-like protein was higher in birds exposed to chronic urban air pollution,
evidence of greater stimulation of phosphatidylcholine secretion and elevated levels of
pulmonary surfactant. This finding suggests that pigeons exposed to urban air pollution
suffer from respiratory distress [Cuesta et al., 2005].

In Johannesburg, South Africa, Steyn and Maina [2015] found that house
sparrows (Passer domesticus), Cape Glossy Starlings (Lamprotornis nitens), and laughing
doves (Streptopelia senegalensis) exposed to urban air pollution had a greater number
of free surface macrophages in the lungs than those from rural areas. Macrophages play
an important role in immune response by destroying or sequestering foreign
particulates and aerosols. The doves exhibited the greatest numbers of macrophages,
followed by the starlings, while the sparrows had the least [Steyn and Maina, 2015].
These results align with observations by Lorz and López [1997], which demonstrated
that domestic pigeons from urban areas had a greater number of macrophages in lung tissue than those from rural sites (Figure 2).

A series of studies conducted at the University of Barcelona in the 1990s sought to study changes in the tracheal epithelium of birds exposed to SO$_2$, NO$_x$, and particulate emissions from coal-fired power plants in northeastern Spain [Llacuna et al., 1993, 1996; Gorriz et al., 1994]. Goldfinches (Carduelis carduelis) exposed to emissions from a power plant showed greater mucus production, a shortening of the cilia in the epithelial cells lining the trachea, and an increase in the number and size of secretory vesicles. These changes to the tracheal epithelium were less pronounced in rock buntings (Emberiza cia) and coal tits (Parus major), which the authors suggest may be attributable to the study design which prevented the goldfinches, trapped in cages, from moving away from the source of emissions [Llacuna et al., 1993]. A related study found abnormal orientation of the cilia in rock buntings and great tits (Parus major) exposed to emissions from a power plant, possibly resulting from increased production of mucus, but not in goldfinches or blackbirds.
(Turdus merula). Normal orientation of cilia helps to clear particles from the airway and support air flow [Gorriz et al., 1994].

C. Case studies

Smoke is known to cause both thermal and chemical damage to avian lung tissue, as well as increase a bird’s susceptibility to respiratory infection [Morris et al., 1986; Verstappen and Dorrestein, 2005; Simone-Freilicher, 2008; Kinne et al., 2010]. Morris et al. [1986] linked exposure to smoke with an outbreak of the contagious respiratory disease laryngotracheitis in a flock of chickens, as well as a short-term increase in mortality and a short-term decline in egg production. Verstappen and Dorrestein [2005] documented the effects of indoor smoke exposure in blue-fronted Amazon parrots (Amazona aestiva aestiva) kept in an aviary. Within hours following exposure, the parrots developed dyspnea, pulmonary edema, and minor damage to their lung tissue [Verstappen and Dorrestein, 2005]. A female ruby blue-headed pionus parrot (Pionus menstruus rubrigularis) showed similar symptoms, as well as weight loss, secondary respiratory infections, and decreased activity after repeated incidences of indoor smoke exposure [Simone-Freilicher, 2008]. Kinne et al. [2010] suggest that carbon monoxide poisoning is usually the cause of death in birds following smoke exposure, but that mycotic air sacculitis, pneumonia, and additional responses to other compounds present in smoke may continue for days or weeks.

Smoke inhalation may also compromise the ability of birds to escape during wildfire events. While the eggs and chicks of ground-nesting species and waterfowl
undergoing molt are thought to be most susceptible to fire events, monitoring of wading bird species in the Everglades showed that even adult, flighted birds may die during wildfires. A fire in April of 1999 caused the death of 50 adult white ibises (*Eudocimus albus*) found on a cattail island. The ibises likely became trapped due to the presence of thick smoke [*Epanchin et al., 2002*].

**III.2 Impaired reproductive success**

In addition to respiratory distress and illness, exposure to air pollutants is also correlated with impaired reproductive success. Reproductive success is a measure of how effective a parent generation is in passing their genes onto subsequent generations, and as such is often assessed by determining not only the number of offspring produced but also the fitness of those offspring.

**A. Controlled exposure**

While previous studies had established that embryos do respond to their gaseous environments, a 1972 study provided further insight into how carbon monoxide (CO) diffusion through the eggshell and inner and outer shell membranes may affect the growth and development of bird embryos. Baker and Tumasonis [1972] found that the hatchability and viability of White Leghorn chicken eggs declined as CO levels increased (Figure 3), and 425 ppm CO was determined to be the critical concentration for these parameters. Vasodilation of blood vessels was noted in embryos
exposed to CO concentrations above 425 ppm. Lactate dehydrogenase (LDH) concentrations in the blood serum also increased in embryos exposed to CO at the critical level, a common indicator of injury or stress. Exposure to higher concentrations of CO also resulted in increased mortality, and exposure to 1,000 ppm CO resulted in 100% mortality. Chicks that hatched following exposure to CO were smaller than control chicks and showed physical abnormalities if exposed during the embryonic stage to CO concentrations above 425 ppm [Tschorn and Fedde, 1974]. Furthermore, the results of this study show that while the eggshell and inner and outer membranes of White Leghorn chicken eggs limit the diffusion of CO, the ability of these layers to protect embryos from CO poisoning appears to degrade with time. Both the age of the egg and the shell condition therefore affect the permeability of an embryonated egg [Tschorn and Fedde, 1974]. If the eggshell and inner and outer membranes of eggs provide only limited protection against elevated concentrations of CO, it is plausible that other atmospheric contaminants might also be able to diffuse through the egg’s layered surface and affect bird embryos.
B. *In situ* exposure

Recent studies in Eastern Europe [Eeva and Lehikoinen, 1995; Belskii et al., 2005] have examined the reproductive success of birds living within air pollution gradients resulting from the operation of copper smelters, as well as the fitness of their offspring. In a study conducted in the 1990s, researchers observed pied flycatchers (*Ficedula hypoleuca*), a migratory species, and great tits, a resident species, at nest boxes constructed at 14 study sites located within an elliptical air pollution gradient surrounding a copper-smelter complex in Harjavalta, Finland. The research team used the heavy metal content of the soil at this industrial site as a proxy measurement for total air pollution exposure associated with operation of the smelter, known to emit sulfur dioxide (SO$_2$) and heavy metals (copper, lead, and nickel). The heavy metal content decreased exponentially with distance from the smelter. The researchers wanted to determine whether or not the reproductive success of these birds was impaired at study sites closer to the copper smelter due to the production of low-quality eggs. This hypothesis was based on previous work showing that exposure to heavy metals and acidifying compounds might impair avian reproductive success by affecting calcium metabolism and reducing the availability of calcium in local food resources, all of which results in eggs with thinner shells [Scheuhammer, 1991; Eeva and Lehikoinen, 1995].

Both the pied flycatchers and the great tits occupying nest boxes at sites closest to the smelter laid fewer eggs, but the pied flycatcher showed an overall greater vulnerability to exposure to industrial air pollution than did the great tit. Hatching
success of pied flycatchers was also dramatically reduced at sites closest to the complex [Eeva and Lehikoinen, 1995]. Production of low-quality eggs did appear to drive the impairment in reproductive success at this industrial site. The eggs of the pied flycatchers were 8% smaller by volume with 17% thinner shells at sites closest to the factory complex as compared to sites located 10 kilometers away, and microscopy revealed that the surface of the eggs collected from sites nearest the factory were more rough and porous [Eeva and Lehikoinen, 1995]. The foraging strategy of the pied flycatcher was suggested to account for its greater sensitivity to industrial pollutants [Eeva and Lehikoinen, 1995]. Later work by this group also found that pied flycatchers, unlike great tits, exhibit stress responses suggestive of a direct toxic effect in the vicinity of point sources of industrial air pollution [Eeva et al., 2000].

The impacts of heavy metal and SO₂ emissions from a copper-smelting plant on pied flycatchers were also studied in Russia by Belskii et al. [2000, 2005]. Results from these studies indicate that reproductive success is impaired at nesting sites closest to point sources of industrial emissions [Belskii et al., 2000, 2005]. At nests at least 15 kilometers from the copper smelter, clutch size increased by a factor of 1.5, and both the number of hatched chicks and the number of fledglings per nest doubled compared to nests located in the nearby vicinity of the plant. At those sites closest to the plant, egg mortality was also 3.5 times greater [Belskii et al., 2005]. In addition, the results of this study showed that the proportion of nestlings infested by parasitic fly larvae as well as the severity of infestation (as measured by the average number of fly larvae per infested chick) increased with decreasing distance to the plant. Higher liver indices,
reduced hemoglobin concentrations, and greater proportions of immature erythrocytes (red blood cells) in nestlings were linked to both the direct toxic effect of air pollutants and greater incidence and severity of parasitic infestation, leading the authors to suggest that exposure to industrial air pollution leads to a general weakening in nestlings, rendering them more susceptible to infestation and subsequent infection [Belskii et al., 2005].

Fortunately, Eeva and Lehikoinen [2000, 2015] show that reducing industrial emissions from point sources improves the reproductive success of birds living nearby. As emissions at the copper-smelter in Harjavalta declined, both the clutch size and the number of fledglings per nest increased [Eeva and Lehikoinen, 2000, 2015]. These findings support previous work in Eastern Europe linking exposure to air pollution with impaired reproductive success in birds.

III.3 Increased detoxification effort, elevated stress levels, and immunosuppression

Laboratory and field studies have also determined that exposure to air pollutants results in increased detoxification effort and elevated stress levels in birds, providing further evidence of the negative health impacts of air pollution on avian species. This research also shows that the avian immune response may be impaired following acute or chronic exposure to air pollution, giving added weight to the previous discussion of how birds exposed to health-damaging air pollutants may be
more susceptible to respiratory disease (see section III.1 Respiratory distress and illness).

A. Controlled exposure

Inhalation exposure to air pollution may increase the stress response and detoxification effort in birds [Cruz-Martinez et al., 2015b]. Sulfur dioxide (SO₂), nitrogen dioxide (NO₂), and volatile organic compounds (VOCs) are the major air pollutants associated with oil sands operations, an important point source of air pollution. VOCs are a class of chemicals that contain carbon and hydrogen, many of which are associated with direct human health impacts, especially cancer. To study how emissions from oil sands operations may impact avifauna, researchers exposed Japanese quail and American kestrels (Falco sparverius) to gaseous mixtures of SO₂, NO₂, and VOCs in whole-body inhalation chambers and measured resulting corticosterone (CORT) and 7-ethoxyresorufin-O-dealkylase (EROD) concentrations in blood samples. CORT activity is an indicator of stress, while EROD activity is often used to signal the body’s increased detoxification effort, especially of polycyclic aromatic hydrocarbons.

Japanese quail were randomly assigned to three groups: control (hydrocarbon-free air), low exposure (0.5 ppm SO₂, 0.2 ppm NO₂, 0.6 ppm benzene, and 1 ppm toluene), and high exposure (50 ppm SO₂, 20 ppm NO₂, 60 ppm benzene, and 100 ppm toluene). Quail were exposed to these gaseous mixtures for 1.5 hours each day for 20 days. American kestrels were separated into a control and experimental group and exposed to hydrocarbon-free air and 5.6 ppm SO₂, 2 ppm NO₂, 0.6 ppm benzene, and 1
ppm toluene, respectively, for 1.4 hours each day for 18 days [Cruz-Martinez et al., 2015b].

CORT activity increased and EROD activity doubled in the kestrels exposed to experimental conditions compared to those exposed to hydrocarbon-free air, though these results were not statistically significant. CORT activity increased in the quail in the low exposure group as compared to the control and high exposure groups. These results are characteristic of a hormetic response to toxins, in which low doses of toxins prompt a response that is inhibited at higher doses. There was no statistically significant difference in the detoxification effort amongst quail in exposure trials. Quail, like other species in the Galliformes family, may be more resistant than other avian species to toxic gases [Cruz-Martinez et al., 2015b]. Though the results of this study demonstrate a specific physiological response to elevated levels of common atmospheric contaminants, it is not possible to isolate the response to any of the four distinct compounds the quail and kestrels were exposed to in these trials [Cruz-Martinez et al., 2015b]. Fernie et. al. [2016] also show that exposure to a gaseous mixture of benzene, toluene, NO$_2$, and SO$_2$ might up regulate function of the hypothalamus-pituitary-thyroid axis in kestrels, which could affect the hormonal control of many key activities, including metabolism and reproduction. Additional research is needed to further characterize the role of the thyroid gland in the stress response and detoxification effort in birds following exposure to air pollution [Fernie et al., 2016].
According to a study conducted in 2005 and 2006, exposure to VOCs may compromise the avian immune system [Olsgard et al., 2008]. In 2005, American kestrels caught in the wild near Prince Albert, Saskatchewan, Alberta were divided into two groups: control (breathing grade air) and high exposure (10 ppm benzene and 80 ppm toluene). The kestrels were exposed to these gaseous mixtures for one hour each day for 28 days. In 2006, captive kestrels were assigned to one of three groups: control (breathing grade air), low exposure (0.1 ppm benzene and 0.8 ppm toluene), and high exposure (10 ppm benzene and 80 ppm toluene). The kestrels were exposed to these gaseous mixtures for 1.5 hours each day for 27 days. The results of this study indicate that while the humoral immune response might not be impacted by inhalation exposure to VOCs, the cell-mediated immune response is suppressed in kestrels exposed to gaseous mixtures of benzene and toluene, at both the low dose and high dose levels [Olsgard et al., 2008]. These findings support earlier studies indicating that exposure to air pollution may increase the risk of respiratory infection in birds.

B. *In situ* exposure

Exposure to industrial air pollution has been linked to genotoxic effects in birds [Baesse et al., 2015], including higher rates of heritable genetic mutations [Yauk and Quinn, 1996; Yauk et al., 2000; King et al., 2014]. Industrial emissions have also been associated with the bioaccumulation of heavy metals in the tissues of vital organs of birds that occupy habitats near point sources of air pollution [Llacuna et al., 1995; Hui, 2002; Burger and Gochfeld, 2000; Lovett et al., 2009; Berglund et al., 2011]. The uptake
of lead in particular has been shown to affect the behavioral development of chicks and negatively impact their growth and survival rates [Burger and Gochfeld, 2000], while avian exposure to mercury is correlated with neurological damage and impaired reproductive success [Scheuhammer, 1991; Lovett et al., 2009].

A 1996 study focused on characterizing hematological changes in great tits, rock buntings, and blackbirds exposed to emissions from power plants [Llacuna et al., 1996]. The study found that exposure to industrial emissions from a coal-fired power plant decreased erythrocyte counts by 11.4% in great tits and by 16.2% in rock buntings. Erythrocytes were also noticeably larger. This is likely due to the immune system's targeted destruction of defective erythrocytes and rapid production of new, immature erythrocytes, which are bigger. Blackbirds also showed statistically significant weight loss and greater concentrations of transaminases, a symptom indicative of liver disease. Plasma samples from rock buntings captured near the power plant also showed a decrease in beta-globulins, indicative of infection [Llacuna et al., 1996].

Industrial air pollution associated with oil sands activity may also negatively affect the health of avifauna. A recent study by Cruz-Martinez et al. studied detoxification effort and immune response in tree swallow nestlings (Tachycineta bicolor) at sites near oil sands operations [2015a]. Exposure to elevated concentrations of ambient air pollutants associated with oil sands activity was linked to increased detoxification effort and suppression of cell-mediated immunity [Cruz-Martinez et al., 2015a].
Exposure to high levels of urban air pollution was found to increase concentrations of elemental toxins in the tissues of vital organs in wild birds, including starlings, owls, crows, and pigeons, captured in Lahore, Pakistan. The magnitude of this increase varied by tissue type and species. Researchers also noted symptoms of degeneration and necrosis of liver tissue in captured birds [Ejaz et al., 2014].

Findings from a study of pigeons in the city of Milan, Italy indicate that porphyrin concentrations in bird excrement and blood methemoglobin levels may serve as useful bioindicators of urban air pollution. Results from this study showed that excreta collected from the pigeons exposed to urban air pollution had significantly higher total porphyrin concentrations and greater proportions of protoporphyrins compared to that collected from control pigeons. Methemoglobin levels were also higher in blood samples collected from the urban birds. This was one of the few studies we discuss in our review that included measurements of ambient air quality, which allowed the researchers to link increased protoporphyrin concentrations in excreta to elevated concentrations of polycyclic aromatic hydrocarbons and higher blood methemoglobin levels to elevated concentrations of ozone and benzene [Sicolo et al., 2009].
III.4 Behavioral changes

Few studies have assessed how exposure to air pollutants may alter bird behavior, but existing research suggests that many different behaviors could be affected, from spontaneous activity to homing.

A. Controlled exposure

Avian exposure to phosphoric acids aerosols may result in changes in activity and weight loss [Sterner, 1993a, 1993b]. A series of studies conducted by Sterner in 1993 was designed to determine if acute exposure to phosphoric acids aerosols affected spontaneous activity such as walking and preening in rock doves (*Columba livia*). Twenty-four rock doves (11 males and 13 females) were exposed to phosphoric acids aerosols at concentrations of 0.0, 1.0, and 4.0 mg/L for 80 min/day for two days. Preening and ambulatory activity were found to significantly decline in the 4.0 mg/L group following the first exposure [Sterner, 1993a]. Sterner’s studies also determined that rock doves exposed to concentrations of 1.0 mg/L and 4.0 mg/L exhibit reduced water intake, food intake, and body weight as compared to control groups, with recovery dependent on both concentration and sex (Figure 4) [Sterner, 1993b].
B. In situ exposure

A recent study also established a connection between behavioral changes and exposure to particulate pollution in cities. It is possible that high concentrations of particulate matter resulting in the haze seen in metropolitan centers may motivate city pigeons to home faster. Further study is needed to determine if this change in behavior is seen in other cities or as a result of exposure to different types of air pollutants [Li et al., 2016].

III.5 Habitat degradation

Industrial emissions often include nitrogen oxides (NO\textsubscript{x}), sulfur dioxide (SO\textsubscript{2}), and heavy metals. Emitted NO\textsubscript{x} and/or SO\textsubscript{2} react in the atmosphere to form nitric and sulfuric acid, which when deposited in wet or dry form contributes to acid deposition (commonly referred to as “acid rain”) and soil acidification. Acid deposition has been

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**Figure 4**: Plot showing mean food intake by rock doves in grams during the pre-exposure (2 days), exposure (2 days), and post-exposure (6 days) periods. The lines represent results from different treatment groups (dotted line: 0.0 mg/L, dashed line: 1.0 mg/L, solid line: 4.0 mg/L). Note that food intake declines in each treatment group, but drops most significantly in birds exposed to the highest level of phosphoric acids aerosols. Recovery in the post-exposure phase depends on concentration [Sterner, 1993b].
hypothesized to contribute to the bioaccumulation of heavy metals in birds [Scheuhammer, 1991; Nybø et al., 1996], possibly by increasing the solubility of elements such as aluminum [Scanes and McNabb, 2003]. Exposure to acid rain also affects calcium and phosphorus metabolism, production of stress hormones, food intake, growth rate, and reproductive success [Scanes and McNabb, 2003]. Acid deposition and heavy metal uptake of soils near point sources of industrial emissions often affects the composition of the plant and invertebrate communities on which birds depend for their food supply [Eeva et al., 1998, 2003; Costa et al., 2011]. Changes in the chemical environment may promote ecological shifts that increase food availability for some species. For example, great tits may have greater reproductive success at sites near point sources of emissions associated with the pulp and paper industry due to higher abundance of caterpillars — a key food resource for this species — in these areas [Costa et al., 2011, 2014]. However, other avian species may suffer if air pollution reduces the quantity or quality of food resources [Eeva et al., 2003].

Changes in food supply may also result in a decrease in the availability of pigment-bearing foods, which in turn could indirectly affect reproductive success by reducing the vibrancy of a bird’s plumage. Faded plumage is a disadvantage for males, as more vibrant, colorful plumage appears to be a sign of good physical condition, rendering males more attractive to potential female mates [Eeva et al., 1998]. Food intake may also be affected by behavioral changes that limit foraging time. Birds may spend less time foraging if tree canopies thin as a result of air pollution, making birds more susceptible to predators [Brotons et al., 1998]. Changes in forest structure or the
composition of local habitat may also affect the prevalence of ectoparasites, which could affect the health of both nestlings and adult birds [Eeva and Klemola, 2013].

III.6 Demographic responses

Research suggests that avian exposure to industrial air pollution may also have demographic consequences. Several studies have linked declines in bird population density [Flousek, 1989; Eeva and Lehikoinen, 1998; Saha and Padhy, 2011; Eeva et al., 2012; Belskii and Belskaya, 2013; Alaya-Ltifi and Selmi, 2014], species diversity [Saha and Padhy, 2011; Eeva et al., 2012; Belskii and Belskaya, 2013; Alaya-Ltifi and Selmi, 2014], and species richness [Belskii and Lyakhov, 2003; Belskii and Belskaya, 2013] to industrial air pollution gradients (Figure 5). Researchers point out that changes in the structure and composition of soils and vegetation resulting from air pollution may affect a number of variables important to the life histories of the birds studied, including food supply and the availability of nesting sites. None of these studies causally linked inhalation exposure to industrial air pollutants to changes in population density, species diversity, or species richness. Within an air pollution gradient, it is difficult to determine how much of the variation in these metrics is due to direct exposure to airborne toxins and how much is due to other abiotic and biotic changes associated with industrial pollution in the local environment [Belskii and Belskaya, 2013]. Noise pollution may also be a confounding variable in assessing the impacts of industrial air pollution on birds, as noise pollution often increases with proximity to industrial sites [Saha and Padhy, 2011].
Air pollution may also indirectly impact the composition of avian communities. Damage caused by air pollution to trees alters the structure of forest ecosystems. While some birds may be able to colonize these habitats, others may make use of ecological niches that are no longer available within that landscape. Over time, this may change the community composition of forests exposed to industrial air pollution [Capek, 1991; Capek et al., 1998; Eeva et al., 2002; Belskii and Lyakhov, 2003; Belskii and Belskaya, 2013]. For example, point counts of bird observations in an air pollution gradient resulting from industrial emissions from the Karabash Copper Smelter in Chelyabinsk Oblast showed that the proportion of canopy-nesting and ground-nesting species in the area increased along the gradient while the proportion of hole-nesting species decreased [Belskii and Belskaya, 2013].

Figure 5: A schematic of an industrial air pollution gradient. The star represents an industrial site. The concentric circles surrounding the star are of increasingly lighter color, illustrating how air pollution and uptake of heavy metals by soils and vegetation decreases with distance from an industrial site. As one moves along this gradient (in the direction indicated by the dotted arrow), population density, species diversity, and species richness increase.
IV. Discussion:

This review finds clear evidence that birds are affected by exposure to a range of reactive gases and particles in the air, including air pollutants with established adverse impacts on human health. Avian responses to air pollution include respiratory distress and illness, impaired reproductive success, increased detoxification effort, elevated stress levels, immunosuppression, and behavioral changes. Key studies elucidating these responses are listed in Table 1, and a map showing locations of where birds in these studies were exposed to air pollution in situ is included in Figure 6. Air pollution may also reduce population density, species diversity, and species richness in bird communities. These demographic consequences are a result of both the direct, toxic effect of exposure to air pollution as well as habitat degradation resulting from poor air quality. Although available evidence consistently suggests air pollution impacts birds, the total number of studies is limited, and important gaps remain.
Figure 6: A map of the locations where birds were exposed to air pollution *in situ* in the studies listed in Table 1.
Table 1: This table lists the 19 studies we identify as key in characterizing individual avian responses to air pollution, including respiratory distress and illness, impaired reproductive success, increased detoxification effort, elevated stress levels, immunosuppression, and behavioral changes. Entries are categorized by both the type of response explored and the type of exposure (controlled or in situ) study specimens were subjected to. A map showing the locations where birds in these studies were exposed to air pollution in situ is included in Figure 6. Additional papers referenced in section III. Key Findings were excluded from this table to focus on demonstrating the range of physiological and morphological

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<th>Respiratory distress and illness:</th>
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<td>Boubou et al., 1991</td>
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<td>Gorriz et al., 1994</td>
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<td>Ejaz et al., 2014</td>
<td>starlings, owls, crows, and pigeons</td>
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<td>Steyn and Maiza, 2015</td>
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<td>Cruz-Martinez et al., 2015b</td>
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responses documented in the peer-reviewed articles downloaded in our original literature review (see section II. Methods).

Researchers have documented avian responses to both industrial and urban air pollution by studying birds in air pollution gradients and by comparing the characteristics of birds captured from industrial and urban areas to those from less polluted sites. While some studies do include information about atmospheric contaminants at study sites, many do not quantify exposure or nearby ambient concentrations of specific chemicals. Quantitative measures of pollutants are rarely used to characterize the sensitivity of a response to specific contaminants. Rather, most study results reflect a comparison between birds of the same species from more or less polluted sites. While the statistical significance of these comparative studies indicates that air pollution is affecting birds, additional confounding variables such as habitat degradation and changes in diet may also contribute to the responses observed. Without exposure estimates for individual contaminants, there is insufficient data to quantify air pollution risk to wild bird populations.

The main challenge in characterizing birds’ exposure to specific air pollutants is the availability of ambient air pollution measurements for comparison with ecological and biological outcomes. Epidemiological studies of human health risk from air pollution often rely on centrally located ambient monitors as a proxy for individual exposure (e.g. the network of surface air monitors run by the U.S. Environmental Protection Agency). These surface monitors could also support analysis of risks to birds, with sufficient information on species habitat and/or migration patterns. However,
most areas of the world do not have ground-based air pollution monitors, and short-term measurements can be difficult, expensive, and of limited relevance to long-term exposure (depending on the duration of the measurements and the variability of the pollutant). Two additional data sources from the atmospheric chemistry community could supplement in situ chemical measurements for the benefit of ornithologists: chemical transport models (CTMs) and satellite data. Most widely used CTMs provide calculated concentrations of the gas and particulate pollutants discussed in this review, and models have been used to estimate human and vegetation exposure in the absence of in situ measurements. CTMs take information on natural and anthropogenic emissions, with a global example shown in Figure 7, and calculate ambient concentrations based on chemical reactions and meteorological transport. Satellite retrievals also offer promise for health- and ecosystem-relevant pollutants, including nitrogen dioxide, carbon monoxide, and particulate matter, with available global data on a near daily basis going back as far as 1999, depending on the instrument. Laboratory-based risk factors, discussed above, and ambient air pollution concentrations from measurements, models, and/or satellite data could be combined to estimate bird health risk on a local, regional, or global basis.
Figure 7: Map showing total anthropogenic emissions of nitrogen oxides (NOx) in 2008; NOx is emitted by all combustion processes, and thus serves as an indicator of emissions from all fuel types. This map does not show the ambient concentrations of pollutants birds are exposed to, but rather highlights where anthropogenic air pollution would be expected to pose the greatest risk to bird communities. Map created using ECCAD (Emissions of atmospheric Compounds & Compilation of Ancillary Data), maintained by the GEIA (the Global Emissions InitiAtive) based on data included in the Emission Database for Global Atmospheric Research (EDGAR).

While potentially informative, such integration of laboratory exposure studies and ambient pollution estimates would have limitations. Rombout et al. [1991] point out that results from laboratory studies must be interpreted with caution, as these studies often use inhalation chamber techniques, which require that birds are stationary during exposure. In the wild, birds would have higher metabolic rates, which would potentially magnify the negative effects of air pollution on the respiratory system [Rombout et al., 1991; Gorriz et al., 1994]. Sterner [1993a, 1993b] discusses how restricting birds to cages may result in behavioral changes that are not actually due to concentrations of reactive gases and aerosols. He refers to this as the “chamber confinement effect.” Finally, Llacuna et al. [1993] also point out that the results of
laboratory studies examining avian responses to exposure to a single pollutant are important, though not sufficient, in characterizing the impacts of air pollution on avifauna in natural settings, where they are exposed to a combination of atmospheric contaminants of varying concentrations. Some of these same limitations already affect the characterization of air pollution risk to humans, including the challenge of extrapolating laboratory studies to real world conditions (e.g. toxicological results of rats and other non-human species), and isolating the effects of a single pollutant health risk when exposure occurs simultaneously to multiple pollutants.

While physiological responses to exposure to air pollutants may serve as examples of phenotypic plasticity, this is not discussed in the studies cited in this review. The capacity for both phenotypic plasticity and adaptation in response to increased concentrations of near-surface reactive gases and aerosols could inform which species may be at a greater long-term risk to pollution exposure.

As we improve the characterization of air pollution risk to birds, it is important to consider interaction of the chemicals in the air with other aspects of global environmental change, including shifts in land use and climate change [Lovett et al., 2009]. For example, urbanization affects both land use and air quality, and warmer temperatures associated with climate change affect air pollution emissions (e.g. smoke from wildfires) and chemical reactions in the atmosphere (e.g. production of ozone) [Jacob and Winner, 2009].

Of the roughly 10,000 species of birds known worldwide, only a few have been studied to characterize avian responses to air pollution, and the animals used in
laboratory experiments may not be representative of the wild bird species most at risk to air pollution. Future studies should work to identify which species across the globe may be most sensitive to air pollution, as well as how responses to air pollution may change with age and sex. Future research on avian responses to air pollution, especially of endangered species, could inform bird conservation programs and improve management of wild bird populations.

**Works Cited**


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III. Conclusion

Implications for Air Quality Policy

The secondary National Ambient Air Quality Standards (NAAQS) established by the Environmental Protection Agency (EPA) are designed to protect public welfare, including “damage to animals, crops, vegetation, and buildings.” However, an analysis of whether or not these secondary standards are adequate in protecting wildlife from any negative effects associated with exposure to health-damaging air pollutants remains out of reach, given the limited research to date on the impacts of poor air quality on non-human species. To support future work on this important research topic, this thesis summarizes what is currently known about how birds are affected by air pollution. Birds respire more efficiently than any other type of terrestrial vertebrate and are therefore likely more vulnerable than mammals, reptiles, or amphibians to atmospheric compounds with known respiratory effects, such as those regulated by the EPA.

Birds are undoubtedly negatively impacted by exposure to air pollution associated with both urban and industrial activity (see II. A review of air pollution impacts on avian species). However, most field studies designed to assess avian responses to air pollution fail to measure in situ exposure. It is therefore impossible to know if the birds observed in these studies were exposed to ambient concentrations of atmospheric contaminants that exceed the secondary NAAQS or fall below these

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4 [https://www.epa.gov/criteria-air-pollutants/naaqs-table](https://www.epa.gov/criteria-air-pollutants/naaqs-table)
standards. While controlled exposure studies are few in number, they do provide some insight as to what levels of air pollution might pose a risk to birds.

While there is no secondary standard set for carbon monoxide (CO), the EPA has established two primary NAAQS for CO; concentrations of CO are not to exceed a) a 1-hour average of 35 parts per million (ppm) or b) an 8-hour average of 9 ppm more than once a year. Birds, like mammals, are clearly susceptible to CO poisoning, and because they are likely more sensitive to respiratory exposure to reactive gases and aerosols, it is possible that to protect adult birds the secondary NAAQS should be more stringent than the primary NAAQS. However, the hatchability and viability of chicken eggs appears to decline if exposed to ambient concentrations of CO greater than 425 ppm, several times higher than the maximum concentration allowed by the EPA. The secondary NAAQS for CO might therefore be adequate in protecting birds during the embryonic stage.

Laboratory studies also show that pigeons exhibit morphological and physiological changes in the respiratory system following exposure to ozone (O\textsubscript{3}) at concentrations of 50 ppm. The primary and secondary NAAQS set by the EPA require that the annual fourth-highest daily maximum 8-hour ambient O\textsubscript{3} concentration, averaged over 3 years, must not exceed 70 parts per billion. The secondary standard for O\textsubscript{3} is therefore far lower than the O\textsubscript{3} concentrations birds have been exposed to in laboratory settings; therefore, available data is insufficient to determine whether or not the secondary O\textsubscript{3} standard is sufficient in protecting birds.
Studies also show that exposure to sulfur dioxide (SO$_2$) at concentrations as low as 1.4 ppm might impair the avian immune response. The secondary NAAQS for SO$_2$ is a 3-hour average concentration of 0.5 ppm, not to be exceeded more than once each year. The secondary standard for SO$_2$ is therefore lower than the SO$_2$ concentrations birds have been exposed to in laboratory settings, and available data is insufficient to determine whether or not the secondary SO$_2$ standard is sufficient to reduce risks to avian species. Controlled exposure studies have also examined avian responses to gaseous mixtures of SO$_2$, nitrogen dioxide (NO$_2$), and volatile organic compounds, including benzene and toluene, but it is impossible to know from these studies which of these gases caused the observed responses.

Additional research is evidently needed to assess the sufficiency of the secondary NAAQS in protecting birds as a valued component of public welfare. Researchers should focus on identifying responses to both acute and chronic exposure to the six criteria air pollutants regulated by the EPA through the NAAQS, including CO, lead (Pb), O$_3$, NO$_2$, SO$_2$, and fine and coarse particulate matter. Both controlled exposure studies and field studies would be useful in this endeavor, but it is essential that researchers carefully measure in situ exposure to ambient air pollution when conducting field studies in order to compare concentrations of air pollutants with the primary and secondary standards and perform rigorous statistical analysis to pinpoint which pollutant is causing the observed responses.
Additional Policy Recommendations

Limited research on the topic of birds and air quality makes it impossible to definitively determine whether or not the secondary NAAQS are sufficient in protecting birds from the risks associated with exposure to health-damaging air pollutants. However, it is clearly important to have secondary standards in place to safeguard animals, especially birds, from the adverse health outcomes linked to exposure to air pollution. The EPA must continue to carefully review the secondary standards as required by the Clean Air Act, considering the results of new peer-reviewed science from diverse disciplines, including atmospheric science, ecology, and veterinary medicine.

It is also recommended that wildlife managers continue to address other stressors resulting from anthropogenic activity that affect birds and might increase the vulnerability of avian species to air pollution, including urbanization, habitat degradation, and climate change. By alleviating the impact of other environmental stressors on birds, managers will reduce risks associated with exposure to health-damaging air pollutants and support the overall fitness and survival of avifauna.

Future Studies

Future studies on birds and air quality should seek to address the knowledge gaps identified in chapter two of this thesis and inform air quality regulation. This
interdisciplinary research should utilize tools from atmospheric chemistry and ecology to link changes in the chemical environment with avian outcomes.

Ambient concentrations of reactive gases and aerosols are measured using both ground-based monitors and satellite data. Ground-based mass concentration and speciation data is available from the EPA Air Quality System Database. Measurements of air pollutants as observed from space, including aerosol optical depth (AOD) and concentrations of NO₂, CO, and O₃, are available from instruments aboard the orbiting satellites that make up the National Aeronautics and Space Administration (NASA) Earth Observing System. NASA has also developed interactive online tools to help researchers visualize satellite data, including Worldview and Giovanni. Both ground-based data and satellite data are used to inform and improve air quality models, another powerful tool for analyzing air pollution trends across broad spatial scales.

When analyzing isolated air pollution episodes, atmospheric scientists also rely on archived meteorological data, mathematical models, and emissions inventories. Researchers and air quality managers use the Hybrid Single Particle Lagrangian Integrated Trajectory (HYSPLIT) Model, developed by the National Oceanic and Atmospheric Administration (NOAA), to determine whether or not long-range transport may have contributed to a specific air pollution episode. This model computes both backward and forward trajectories of air parcels, allowing air quality analysts to better understand how atmospheric pollutants may have traveled through a given area before and after an event. These simplified trajectories are computed using archived meteorological observations, such as mean wind field, and represent the best possible
estimate of an air parcel's route to or from a specified site over a given period of time. To characterize pollution dispersion from point sources, such as smoke stacks, atmospheric scientists and engineers often use the Gaussian Plume Model. This model is also informed by archived meteorological data. Climate models and climate data visualization tools such as ClimateReanalyzer are useful to both to atmospheric scientists and ecologists in investigating how changes in the atmosphere might affect ecological processes, ecosystems, and public health. Emissions inventories and data visualization tools such as ECCAD: Emissions of atmospheric Compounds & Compilation of Ancillary Data also help air quality scientists to analyze air pollution episodes, build understanding of spatial trends in air pollution, and make management recommendations.

Ecologists use several different sets of citizen science data to assess trends in bird populations, including eBird, Project FeederWatch, the Breeding Bird Survey, and MAPS (Mapping Avian Productivity and Survivorship):

- **eBird** was launched in 2002 by the Cornell Lab of Ornithology and the National Audubon Society. This online reporting tool facilitates the collection of millions of bird observations each year by aggregating checklists submitted by birders around the world. All collected data are filtered automatically to flag any unusual observations, which are then reviewed by local experts. Quality assured data is made available to scientists and wildlife managers to use in research or the strategic planning of conservation efforts.
• **Project FeederWatch** is run by the Cornell Lab of Ornithology and Bird Studies Canada. This program supports citizens in monitoring the birds that visit their feeders during the winter months and enables researchers to track changes in the winter distribution of common bird species.

• The **Breeding Bird Survey (BBS)** is orchestrated by the Patuxent Wildlife Research Center and the Canadian Wildlife Service. The goal of the survey is to monitor trends in the distribution of North American bird populations. Thousands of birders participate in BBS data collection each year. Birders who participate are assigned to a random roadside route and must follow a strict protocol when making observations. Their observations are sent to a team of researchers and statisticians who analyze the data to assess the status of hundreds of bird species in North America.

• **MAPS (Mapping Avian Productivity and Survivorship)** is organized by the Institute for Bird Populations. The institute engages local and state agencies, non-profits, and individuals in collecting demographic data to help explain trends in avian populations. There are over 1,200 monitoring stations associated with MAPS throughout the United States and Canada. By collecting information about the vital rates of birds that visit these stations, researchers are able to assess the underlying cause of the shifts in populations identified in the analysis of other datasets. Vital rates include several key demographic parameters, such as survival, recruitment, residency, and productivity.
Integrating tools from atmospheric science and ecology will help bring environmental science to a new frontier to address emerging conservation questions of global importance. There are many possibilities for future studies.

One idea that has emerged from this thesis is exploring the use of bird feathers as a biomarker for health-damaging air pollutants, such as aerosols or ozone. Isotopic analysis of feathers is already used to study the migratory behavior and diets of birds, and research has shown that feathers serve as useful biomarkers for elemental pollution, persistent organic compounds, and agricultural activity. Atmospheric scientists also use isotopic analysis in studies designed to determine the origin of air pollutants. It therefore might be possible to develop a noninvasive sampling technique to assess avian exposure to air pollutants during molt by analyzing the concentrations of stable isotopes of carbon, hydrogen, nitrogen, and sulfur found in bird feathers.

A second idea for a future study is to conduct a retrospective analysis of one or more of the field studies cited in chapter two of this thesis in order to quantify avian exposure to health-damaging air pollutants using data from both ground-based monitors and satellite instruments. This would allow researchers to compare the actual ambient concentrations of air pollutants birds were exposed to in these studies with standards set by the EPA.

It might also be possible to compare bird observations or demographic data

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5 [http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0137622](http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0137622)


collected by citizen scientists in the years before, during, and after a serious air pollution episode, such as an intense wildfire, to determine if acute exposure had any immediate or long-term effects on populations. This would be the first integration of large-scale atmospheric chemistry and ecology datasets to address the impact of reactive gases and aerosols on non-human species. Ideally, additional research on birds and air quality will enable environmental scientists to determine which species are most sensitive to air pollution. This could be especially important in ensuring additional protections for endangered species.

This thesis constitutes an important first step in linking research findings from diverse disciplines to characterize avian responses to air pollution. However, in order to determine whether or not current air quality regulation is sufficiently stringent to protect birds from the risks associated with exposure to health-damaging air pollutants, additional research must seek to assess the extent of both acute and chronic exposure to reactive gases and aerosols amongst avifauna and the impacts of said exposure on avian physiology and demography. This will require that researchers collaborate with experts outside of their field and pull in tools from numerous scientific disciplines. Research on this topic will therefore inform policy and wildlife management as well as improve communication between fields of study, creating new opportunities in interdisciplinary environmental science.