

Guano Rain and Growing Pain: Co-nesting Dynamics of Double-crested Cormorants and

Black-crowned Night-herons at Tommy Thompson Park

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Abstract

This study investigates the co-nesting dynamics between double-crested cormorants (*Nannopterum auritum*) and black-crowned night-herons (*Nycticorax nycticorax*) in Tommy Thompson Park, Toronto, Canada, from 1992 to 2023. Linear mixed models with Bayesian inference were used to examine the impacts of cormorant abundance, nest density, management practices, and environmental factors on night-heron population growth.

The strongest and only statistically significant relationship was a positive association between cormorant and night-heron growth indices. Results showed substantial uncertainty in the effects of most variables on night-heron growth indices, with wide credible intervals for nest densities, night-heron road proximity, and management activities. Nest densities of both species and proximity to roads had minimal effects on night-heron colony growth, with posterior means near zero. Management activities showed a slight positive but non-significant effect on night-herons. The study revealed that while cormorant population growth generally benefited night-herons, there was high uncertainty in parameter estimates, potentially due to small sample sizes and ecosystem complexity.

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Thesis Structure

This thesis is divided into a literature review and a paper to capture the main research of the thesis *Guano Rain and Growing Pain: Co-nesting Dynamics of Double-crested Cormorants and Black-crowned Night-herons at Tommy Thompson Park*. Some duplication will occur between the Introduction to this thesis and the Introduction and Methods outlined in the paper, which will be indicated with footnotes. Following the main thesis paper is a smaller reflection paper to capture the challenges of working with significant data over long periods of time as well as working with ecological modelling using Bayesian inference as a graduate student new to the methodology.

Chapter One: Literature Review¹

Overview of Habitat Impacts near Cormorant Colonies

Studies have examined the impacts of waterbird nesting including cormorants, night-herons, great egrets (*Ardea alba*) and snowy egrets (*Egretta thula*) on nesting habitats (see Craig et al., 2012; Dias et al., 2012; Hebert et al., 2005; Klimasyk et al., 2015). In New York Harbour, Craig et al. (2012) examined leaf litter characteristics, plant and arthropod community structure, and soil at colonised and non-colonised sites on two islands. Near double-crested cormorant (*Nannopterum auritum*, hereafter cormorant) colonies, plant species richness and total plant cover were reduced and there was a shift in arthropod community structure from plant feeders to carrion feeders and scavengers under established, high density cormorant colonies. However, no significant impacts on overall richness and abundance of arthropods was observed. Documented impacts increased with older, more established colonies due to density and size. Wading-bird colonies and colonies that were more recently established were smaller and less dense, and so had fewer ecological impacts. Plot comparisons did not indicate significant differences between cormorants and wader impacts, despite the fact that cormorants are assumed to have greater impacts on their habitat. High nutrient output from cormorant guano under cormorant nests can coat lower branches and vegetation, inhibiting photosynthesis and transpiration (Sobey & Kenworthy, 1979; Ellis et al., 2006).

Further investigations by Klimasyk et al. (2015) into the ecological effects of great cormorant (*Phalacrocorax carbo*) colonies have found that extreme nutrient deposition from cormorant guano led to significant soil chemistry and plant vegetation alterations, including the increase of nitrophilous and invasive plant species. These nutrient changes persisted in peripheral

¹ This literature review has been adapted from the research proposal submitted for this thesis.

or abandoned colony sites in concentrations at least seven times higher than control plots, and plant species richness remained low at former sites with few trees surviving. Large loads of nitrogen and phosphorus transferred to the nearby lake through surface runoff, leading to the fertilisation of littoral areas and promoting phytoplankton growth. Groundwater was found to contain organic matter, nitrogen and phosphorus. Coliform bacteria numbers in the littoral zone (the shallower area of the lake proximal to the colony that contains high oxygen and sunlight nutrients) also increased because of runoff (Klimaszyk et al., 2015). While cormorants can feed on a relatively large area up to 30 km away from the colony, the majority of their waste is deposited in the small area under the colony and near the lakeshore (Klimaszyk et al., 2015).

History of Cormorant Populations in North America

Cormorant colonies censused between 1990s-2000 at 190 sites showed increases of nests from approximately 21,000 to 76,000 over four censuses, with annual average growth rates higher between 1980-1990 and lower between 1990-2000 (Weseloh et al., 2002). This extraordinary growth has been documented through a joint Canadian-US conservation program that censused all waterbird colonies on the Great Lakes every 10 years up until 1999. Around Lake Ontario, there were ten active colonies with 6,746 nests in 1990 and 17 active colonies in the following years with nest numbers growing between 13.7-21.4% per year (Weseloh et al., 2002). The purpose of Weseloh et al.'s (2002) study was to identify all cormorant colonies in the Canadian Great Lakes and United States colonies that may be crossing borders in order to look for broader population trends in the area over time. The authors asserted this data should provide sufficient information for wildlife managers in the area to make evaluations of the distributions and population trends of cormorants in their areas, information fundamental to management decisions regarding cormorants (Weseloh et al., 2002).

As cormorant populations have increased since reaching low levels in the 1970s, wildlife managers and policymakers have often worked under the assumption that populations are overly abundant; Wires and Cuthbert (2006) have shown that historically, colonies recorded prior to the 1900s may have been much larger than what currently exists. Wires and Cuthbert (2006) suggest that the perceived overabundance being described by wildlife managers and policy may be the “social carrying capacity”, or what may be tolerated by human communities, which may be far narrower than the biological carrying capacity for this species. Because historically large populations have existed for cormorants, population targets based on fisheries or human value objectives will require intensive management practices (Wires & Cuthbert, 2006). The authors highlight how management programs reducing cormorant populations do not address underlying impacts to fish populations across the continent and are at odds with broad scale conservation initiatives. They suggest pursuing programs based on the acknowledgement of complex needs for ecosystem health in which humans, cormorants and fish are only a small number of species driving interactions (Wires & Cuthbert, 2006).

Interspecific Interactions between Co-nesting Waterbirds

Cormorants are thought to negatively affect co-nesting colonial waterbirds by destroying vegetation used as nesting sites and usurping limited habitat. Cuthbert et al. (2002) studied the potential impacts of cormorants on great blue herons (*Ardea Herodias*, a wading colonial waterbird) and black-crowned night-herons (*Nycticorax nycticorax*; hereafter night-herons) in the Great Lakes region by examining population trends, interspecific interactions, and cormorant impacts on vegetation in tree-nesting colonies. Data were collected on waterbird population trends to estimate regional population size, breeding colony size, and habitat used by colonial waterbirds in the U.S. area of the Great Lakes. Trends were analysed in wader colony

populations to determine independence from cormorant populations. Population trends of blue herons and night-herons did not indicate negative impacts by cormorant populations as they increased. While cormorants have caused vegetation loss at a number of sites - partial or complete - site data such and field observations of interspecific interactions indicated the presence of cormorants did not cause blue heron or night-heron declines or abandonment except under rare circumstances (Cuthbert et al., 2002). This suggests that cormorant control policies (e.g., lethal control, egg oiling, hazing nesting birds) are not justified in their assumption of negative impacts of cormorants without further evidence and careful documentation (Cuthbert et al, 2002; McDonald et al., 2018; see Wyman & Cuthbert., 2015, below).

Studies have examined how nest location, nest density, and species identity drive agonistic interactions in mixed-species waterbird breeding colonies. Previous investigations have focused on cormorant interactions with other species within homogenous breeding environments, making broad patterns difficult to identify (see Arevalo Ayala, 2022; Cuthbert et al., 2002; Wojczulanis et al., 2005). Wyman & Cuthbert (2015) studied agonistic interactions specifically among cormorants and great blue herons nesting both on the ground and in trees across two study sites to determine how species identity and habitat structure relate to agonistic interactions among nesting individuals. Most agonistic interactions were intraspecific interactions among cormorants; but great blue herons engaged in higher interspecific and intraspecific interactions when nesting near cormorants.

Interspecific territoriality may reduce reproductive success and there have been concerns that cormorants will reduce reproductive success of co-nesting colonial waterbirds, but evidence of these negative effects remains inconclusive (see Cuthbert et al., 2002; Jarvie et al., 1997; Shieldcastle & Martin, 1997; Skagen et al., 2001; and Somers et al., 2011.) Wyman and

Cuthbert's (2015) observations (supported the hypothesis proposed by Somers et al. 2011) that species identity and habitat structure influence the rate of agonistic interactions among nesting individuals, and that arrangement of nests within the colony matters as much as overall composition (as the species of neighbours also had a strong influence on agonistic behaviour). While Wyman and Cuthbert (2015) suggest great blue heron behaviour changes in presence of cormorants, they do not provide sufficient evidence to either support or discourage management of cormorants. The authors highlight that reproductive impacts and potential impacts of cormorant control activities must also be considered (Wyman & Cuthbert, 2015).

Other Impacts to Colonial Waterbird Populations

Factors such as species interactions, environmental change, and human activity can impact nest success and populations of colonial waterbirds. Skagen et al. (2001) looked at tree-nesting colonies of blue herons and cormorants to highlight how species interactions and environmental change can mask or intensify the impacts of human activity on waterbird populations. Changes at a wildlife viewing area of blue herons and cormorants, including the decline of active blue heron nests and nest success, pointed to a combination of impacting factors including habitat changes such as tree falls, usurpation of nests by cormorants, and human disturbance. Blue heron nests most vulnerable to flooding, rain and wind impacts experienced greater nest failure. The study site was completely abandoned by blue herons by the end of the study and a new colony was documented one kilometre away. No evidence was found of decline of cormorants in the wildlife viewing area, but habitat changes and adverse weather did contribute to nest failure (Skagen et al., 2001). This study highlights the importance of considering multiple factors when examining population trends of colonial waterbirds, including

human disturbance, exposure to negative weather events, habitat changes, and interspecific competition.

Waterbirds in the Great Lakes Region

Wyman et al. (2018) examined how cormorant abundance and management affected colony growth of four co-nesting waterbird species in the North American Great Lakes from 1976-2010. Using data from waterbird surveys and cormorant management records, they modeled the relationships between cormorant factors and colony growth indices for great blue herons, night-herons, ring-billed gulls (*Larus delawarensis*), and herring gulls (*Larus argentatus*). The authors found that responses varied by species. Ground-nesting gull species showed positive associations with cormorant abundance and management presence. In contrast, tree nesting night-herons had negative associations with both cormorant abundance and increasing management intensity. Blue herons showed little response to cormorant factors overall.

Wyman et al. (2018) found evidence that cormorant management (i.e., lethal removal of cormorants from a site) was not uniformly beneficial or neutral for co-nesting waterbirds, contrary to common assumptions. The authors suggested that cormorant management needs to account for likely effects on co-nesters, especially species of conservation concern like night-herons. They recommended conducting management at night when possible to minimize gull predation of cormorant nests (ground-nesting colonies) and carefully considering management activities and presence near nesting black-crowned night-herons (tree-nesting colonies). Similar to Skagen et al. (2001), their research demonstrated the importance of examining community-level impacts when managing abundant species while highlighting the

complex dynamics between cormorants, their management, and other colonial waterbirds in the Great Lakes ecosystem.

Cormorant-Human Conflict and Management Implications

Cormorants are a bird that have frequently come into conflict with human interests, including fisheries and public desire to protect trees (McDonald et al., 2018). There is a history of the extinction of persecuted birds in North America, starting with the disappearance of the passenger pigeon in 1914- a bird once so numerous that its extinction was considered impossible (Wires, 2015). Cormorants have faced what Wires (2015) calls “institutionalised persecution” historically, a centuries-long conflict with humans that was codified into federal depredation laws by the U.S. Fish and Wildlife Services in 2003 and resulting in the destruction of half a million cormorants by 2014 despite insufficient biological evidence supporting the action (Wires, 2015). In Canada during the same time there were no established federal regulations, but provincial legislatures across the country lead to the death of at least 30,000 birds and the oiling of hundreds of thousands of eggs. This practice has only been used twice to benefit or recover fisheries or historical fish communities, specifically in Alberta and Quebec- in Ontario, the management of cormorants relates primarily to ecological concerns around negative habitat impacts and vegetation destruction (Wires, 2015). Tommy Thompson Park (TTP) has used only non-lethal management techniques and Presqu’ile Provincial Park has since shifted to non-lethal management (McDonald et al., 2018). Lethal management has occurred through large-scale shooting and egg oiling in at least two colonies in the province.

Ontario declared a fall hunting season for cormorants commencing in 2020 with a stipulated maximum of 15 birds per hunter per day, a move that has alarmed ecologists and biologists (Hobson, 2021). To date, Canada has destroyed significantly less birds than the US

despite supporting much higher numbers of cormorants in comparison with estimated deaths in the US (Hobson, 2021). This hunt could significantly threaten Ontario's breeding population (Fraser, 2020). Wires (2015) highlighted that despite legal protections being in place in the US, both the US and Canada continue to see policies that do not promote knowledge-based solutions and instead justify the destruction of cormorants in high numbers for merely completing their natural roles as piscivores. TTP's nonlethal management practices have provided a unique model in which diverse stakeholder views and values are considered. This model can be incorporated into the management of other colonies (McDonald et al., 2018).

Cormorants and Night-herons at Tommy Thompson Park

Cormorants arrived at TTP in 1990 and populations increased from six to a peak of 14,515 nesting pairs in 2018 (with some reduction in size since), making it one of the largest non-lethally managed cormorant colonies in North America (McDonald et al., 2018). Toronto Region Conservation Authority (TRCA) used a spatial approach to limit the distribution of tree-nesting cormorants with the objective of minimising tree mortality (McDonald et al. 2018). Practices adopted in 2008 to encourage ground-nesting over tree-nesting were successful, showing significant reductions in tree-nesting cormorants. Since 2018, cormorant populations have been in a mild decline, with roughly 80-90% of the population of the park now ground-nesting on Peninsula B (A. Chreston, personal communication, January 26 2025; McDonald et al., 2018)².

Using this spatial strategy, managers at TTP focused on Cormorant Conservation Areas (ground-nesting areas) and Cormorant Deterrence Areas (primarily healthy tree areas) to

² Since the publication of McDonald et. al. (2018), cormorants moved to the nearby Toronto Island Park, with roughly 1,267 nests present in 2024. As of 2024, tree-nesting counts for cormorants were at 596, the lowest number of tree nests since the 1990s, with night-herons still absent from the park (A. Chreston, personal communication, February 10, 2025; G.S Fraser, personal communication, January 9, 2025).

determine where cormorant nesting should be allowed or discouraged (McDonald et al., 2018). In Cormorant Conservation Areas, conspecific attraction experiments were undertaken to encourage ground-nesting through methods such as providing hay for nesting materials, moving knocked-down trees nests to ground-nesting areas, decoy cormorants and vocalization broadcasts, and providing old tires as uniform structure for nests. Deterrence activities in tree-nesting areas included an escalating scale of techniques based on cormorant responses (with varying levels of movement, noise, or nest interference and removal). Annual monitoring of tree nests numbers and locations has occurred since 1992 (see Jarvie et al., 1997; Rosenberger et al., 2015). The success of these non-traditional non-lethal management methods shows that vegetative damage and public conflicts can be reduced by using a spatial approach to limit the distribution of cormorants and promote ground-nesting over tree-nesting within the colony (McDonald et. al, 2018).

Night-herons started nesting at TTP in 1979 (Wilson & Cheskey, 2001). The population peaked in 2000 at 1,265 nests (TRCA unpublished data). Night-heron nests were counted annually starting in 1979, and Fraser followed a sample of nests as part of a monitoring program to track nest success and possible causes of nest failure from 2010-2019 (Gentile 2022, Fraser unpublished data). Night-heron nest counts started declining in 2000 and the species was absent by 2022. Between 2010-2019, nest success declined over time with predation by raccoons (*Procyon lotor*) as the suspected mechanism influencing night-heron populations. As TTP is a peninsula connected to Toronto, it is unlikely that raccoon management techniques will reduce predation on night-herons, and small colony sizes prevent nesting birds from protection in density. Attempts at deterring predators (with predator guards around trees) proved unsuccessful, with no difference between nest successes for protected or control trees (Gentile, 2022).

The Great Lakes Colonial Waterbird Census 1977-2009 indicated that the average night-heron colony size has declined by 75% within a thirty-year period in Canada, and by 57% in the United States (Weseloh et al., 2022). Gentile (2022) compiled night-heron conservation status in eastern North America, where it is classified as *threatened* or *low concern* depending on the region, is listed as threatened under the Species at Risk assessment in the United States, and classified as a species at risk in all states east of the Mississippi River. The most significant threat to night-heron populations across jurisdictions is likely habitat loss due to human disturbance (Gentile, 2022).

Using TTP's dataset, Jarvie et al. (1997) found that there was a relationship between expanding nest areas of cormorants and the receding nest areas of night-herons at two peninsulas. They used spatial data (tree coordinates) and attribute data (annual nest counts, tree diameter at breast height) integrated into ArcGIS with a shoreline layer and georeferenced aerial photographs to analyse nest distributions of the two species with ten years of data at the time. Jarvie et al.'s (1997) GIS mapping of two peninsulas in TTP showed clear cause-and-effect relationships between cormorant colony expansion and night-heron colony recession, though they did not try to determine mechanisms involved. The authors predicted that cormorants would completely overtake the woodlands at Peninsula B as they already had on Peninsula A, and that night-herons would abandon those areas and restrict themselves to Peninsula C. They further predicted that cormorants would eventually nest on Peninsula C and possibly Peninsula D in the future, leading to further processes of colonisation and competition.

Further collected data by the TRCA and analysis done up to 2011 showed that Peninsulas B and C had indeed been colonised further by cormorants, with night-herons still nesting on both peninsulas but in significantly lower numbers. (TRCA unpublished data). Rosenberger (2015)

found through spatial analysis and observations that cormorants seemed to play a role in the decline of night-herons at TTP through indirect effects with stronger impacts on Peninsula C, where cormorants were more likely to occupy trees with night-heron nests, and with negligible effects on Peninsula B. Rosenberger (2015) found that these results contradicted previous conclusions reached by Jarvie et al. (1997), who found that cormorants caused night-heron declines on Peninsula B.

Chapter Two: Co-nesting Dynamics of Double-crested Cormorants (*Nannopterum auritum*) and Black-crowned Night-herons (*Nycticorax nycticorax*): A 31-Year Study at Tommy Thompson Park

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Keywords

Phalacrocorax auritus, *Nycticorax nycticorax*, double-crested cormorant, population growth, black-crowned night-heron, co-nesting dynamics

***Abstract*³**

This study investigates the co-nesting dynamics between double-crested cormorants (*Nannopterum auritum*) and black-crowned night-herons (*Nycticorax nycticorax*) in Tommy Thompson Park, Toronto, Canada, from 1992 to 2023. Linear mixed models with Bayesian inference were used to examine the impacts of cormorant abundance, nest density, management practices, and environmental factors on night-heron population growth.

The strongest and only statistically significant relationship was a positive association between cormorant and night-heron growth indices. Results showed substantial uncertainty in the effects of most variables on night-heron growth indices, with wide credible intervals for nest densities, night-heron road proximity, and management activities. Nest densities of both species and proximity to roads had minimal effects on night-heron colony growth, with posterior means

³ This abstract is duplicated from the introduction to this thesis.

near zero. Management activities showed a slight positive but non-significant effect on night-herons. The study revealed that while cormorant population growth generally benefited night-herons, there was high uncertainty in parameter estimates, potentially due to small sample sizes and ecosystem complexity.

Introduction

Colonial breeding can be observed in many species, with reptiles, mammals and birds all exhibiting this behaviour. Specific to birds, coloniality is a breeding arrangement where individuals or pairs nest in close proximity to others, forming a spatially clumped distribution (Coulson, 2002). To constitute coloniality, nests are significantly closer to each other than if it were unintentional, with birds often retaining the same neighbours across breeding seasons, allowing for complex interactions and behaviours to develop among individuals (Coulson, 2002). Waterbirds (in conservation, birds that are dependent on or inhabit bodies of water or wetland areas) commonly use colonial breeding as a primary breeding strategy, with 98% of waterbird species breeding this way (Varela et al., 2007). With predation accounting for 80% of nest failures in birds, breeding in colonies may afford some protection for species (Varela et al., 2007). While colonies will inevitably attract predators through visual, auditory, and olfactory cues, breeding in large numbers reduces per-individual risk and groups may be able to better detect and deter predators (Roberts, 1996; Robinson, 1985; Varela et al., 2007). Though some benefits may accrue through coloniality, colonial waterbirds may also experience negative effects including increased spread of disease and parasitism, attraction of predators, and increasing interference by humans for management or other purposes (Danchin & Wagner, 1997).

Birds may also nest in mixed-species colonies with co-nesting species impacting each other through indirect or direct mechanisms. Direct mechanisms involve interactions between

individuals of two species while indirect mechanisms are mediated through an external factor or third organism (Moon & Moon, 2011). Waterbirds may nest in mixed-species colonies in order to acquire resources or for additional predator protection (see Nuechterlein, 1981; Wojczulanis et al., 2005), but competition for resources or aggressive interspecies interactions may favour the success of one species over another or cause a species to abandon an area (see Ellis & Good, 2006; Gorski & Pajkert, 1997; Jarvie et al., 1997; Somers et al., 2011; Varela et al., 2007).

Double-crested cormorants (*Nannopterum auritum*, hereafter cormorants, Figure 1) are a widely distributed species of colonial waterbirds in North America. After population levels nearly reached extinction in the 1970s through a possible combination of the effects of toxins on nest success and human exploitation or conflict, legislation banning pesticides and an increase in focus on cormorant management led to a population boom (Hatch, 1995; Weseloh et al., 2002). Migratory populations in the Great Plains, Great Lakes and Atlantic Coast doubled every five years for decades (Dorr et al., 2021; Price & Vaughn Weseloh, 1986), and Tyson, et al. (1999) estimated most reside in the interior and Atlantic regions (see also Dorr et al., 2021). However, Wires and Cuthbert (2006) argued their populations are lower than those in early European settlement and recent populations have likely leveled off or even declined (Guillaumet et al., 2014; Wyman et al., 2016).



Figure 1. Double-crested cormorants at Tommy Thompson Park, Toronto, Ontario.

Photograph by G.S. Fraser.

Cormorants nest in large colonies throughout their breeding ranges, with surveyed numbers ranging from 1 - 8,400 pairs in a colony and with a preference exhibited for nesting on small rocky or sandy islands (Dorr et al., 2021; Meier, 1981). Cormorants demonstrate high nesting plasticity, nesting in both trees and on the ground (Dorr et al., 2021). Management of cormorant colonies across North America often relies on lethal techniques such as culling and egg oiling (U.S. Fish and Wildlife Service, 2020), though some colonies are managed non-lethally with methods to deter tree nesting while encouraging ground-nesting, such as noise deterrence and nest removal (McDonald et al., 2018).

Cormorants may co-nest with several colonial waterbird species. In the interior region, it may include ring-billed gulls (*Larus delawarensis*), herring gulls (*Larus argentatus*), and American white pelicans (*Pelecanus erythrorhynchos*) on the ground; and great blue herons

(*Ardea herodias*), and black-crowned night-herons (*Nycticorax nycticorax*, hereafter night-herons) in trees (Skagen et al., 2001; Somers et al., 2007, 2011; Wyman & Cuthbert, 2015). Cormorants may negatively impact co-nesting waterbird species through direct mechanisms such as aggressive interactions, nest usurpations, or competing for nesting territory (Cuthbert et al., 2002; Jarvie et al., 1997; Skagen et al., 2001; Somers et al., 2011), but evidence of negative effects of cormorants on co-nesting waterbirds remains inconclusive with some species seeing no population impacts (Wyman & Cuthbert, 2015). Somers et al. (2011) hypothesised that variability in intraspecific population impacts between cormorants and co-nesting species could be determined by habitat structure, nest density, and the species involved.

It is important to acknowledge that while cormorants may impact local waterbird species, some studies have found that the management of cormorants also impacts night-heron populations (Wyman et al., 2018). Negative effects on night-heron populations by cormorants have been recorded and this may be cited as a reason for cormorant colony management practices; however, other datasets lacked clear relationships (see Somers et al., 2011) while still others have found a negative relationship between increased management visits for cormorant colonies and night-heron colony growth, suggesting that human disturbance occurring during the management of cormorants may have more impact on night-herons than the cormorant colonies themselves (Wyman et al., 2018).

In the interior region, night-heron (Figure 2) populations have been relatively stable in North America since the banning of DDT in the 1970s. However, some regions are seeing decline of night-heron populations, and they have been listed as threatened or endangered in certain areas of the United States (Scarpignato et al., 2021). Night-heron populations in Canada have seen large decreases of up to 70% since the 1970s, but population trends have stabilized

over the last decade (The State of Canada's Birds, 2024). It is estimated that Canada is home to approximately 9,200 breeding individuals out of a global population of 3,000,000 night-herons (The State of Canada's Birds, 2024). Data for population of status from Breeding Bird Surveys for night-herons may be unreliable due to the birds' crepuscular to nocturnal activity and colonial breeding, which is not ideal for Breeding Bird Survey assessments (The State of Canada's Birds, 2024).



Figure 2. A Black-crowned Night-heron in its nest in Tommy Thompson Park, Toronto, Ontario. Photograph by G.S. Fraser.

Wyman et al. (2018) examined cormorant management impacts on co-nesting species and found a negative relationship between cormorant abundance, cormorant management and night-heron colony growth (an index value calculated to indicate increases, decreases, or no changes in colony size from one survey to the next). They hypothesised an indirect effect from

cormorants: increased nutrient output from cormorant guano ‘rain’ damages the understory vegetation that night-herons nest in almost exclusively (see also Shieldcastle & Martin, 1997; Skagen et al., 2001; Wires & Cuthbert, 2006). However, the increased presence of cormorants does not have a predictable relationship with the decline of other tree-nesting waterbirds and there is limited evidence that cormorants cause significant displacement of other birds (Cuthbert et al., 2002; Jarvie et al., 1997; Shieldcastle & Martin, 1997; Somers et al., 2011). Cuthbert et al. (2002) suggested that cormorant presence had not caused night-heron declines, and that cormorant management and control should not assume potential impacts on co-nesting waterbird species without documentation.

Colonial Co-Nesting Waterbirds at Tommy Thompson Park

Tommy Thompson Park (TTP) is a designated Environmentally Significant Area and a globally significant Key Biodiversity Area (McDonald et al., 2018; Figure 3). Hundreds of migratory species of birds visit the park each year, as well as many other species of non-migratory animals that rely on TTP as their habitat. As an urban wilderness, management of TTP by Toronto and Region Conservation Authority (TRCA) focuses on maximising biodiversity, preserving significant species, and enhancing habitat within its borders (McDonald et al., 2018). These goals were challenged by the cormorant population growing exponentially since its arrival in 1990, leading to the death of trees and vegetation in surrounding areas and significant changes in their habitat (Taylor et al., 2011). In the development of a cormorant management plan – through a cormorant advisory group – it was suggested that cormorants may be causing the decline in other co-tree-nesting waterbirds (Taylor et al., 2011); a hypothesis often used to justify lethal management methods in other jurisdictions with little evidence to support it (see Hobson, 2021; Wires, 2014; Wyman et al., 2018).



Figure 3. Tommy Thompson Park in Toronto, Ontario, with research area and peninsulas indicated.

TTP is unique in its cormorant management practices, using only non-lethal management methods since the species arrived (McDonald et al., 2018). Cormorant populations increased exponentially from six in 1990, peaking at 14,515 in 2018 and down to 8,860 in 2022, making it one of the largest non-lethally managed cormorant colonies in North America (McDonald et al., 2018; Figure 4). Cormorants have reduced forest cover and spread over a large area within TPP

since their arrival, with ground or tree-nesting cormorants present on peninsulas A, B, and C (McDonald et al., 2018; Taylor et al., 2011). Tree-nesting night-herons arrived in TTP in 1979, prior to the arrival of cormorants (TRCA unpublished data) and the area came to be considered an important breeding area for night-herons (Rush et al., 2015). Night-herons have declined from a population high within TTP of 1,235 to 82 between the years 2000 and 2021, and in 2022 were absent at the park for the first time since 1990 (TRCA unpublished data; Figure 4). What caused that decline is unknown, but cormorants are suspect.

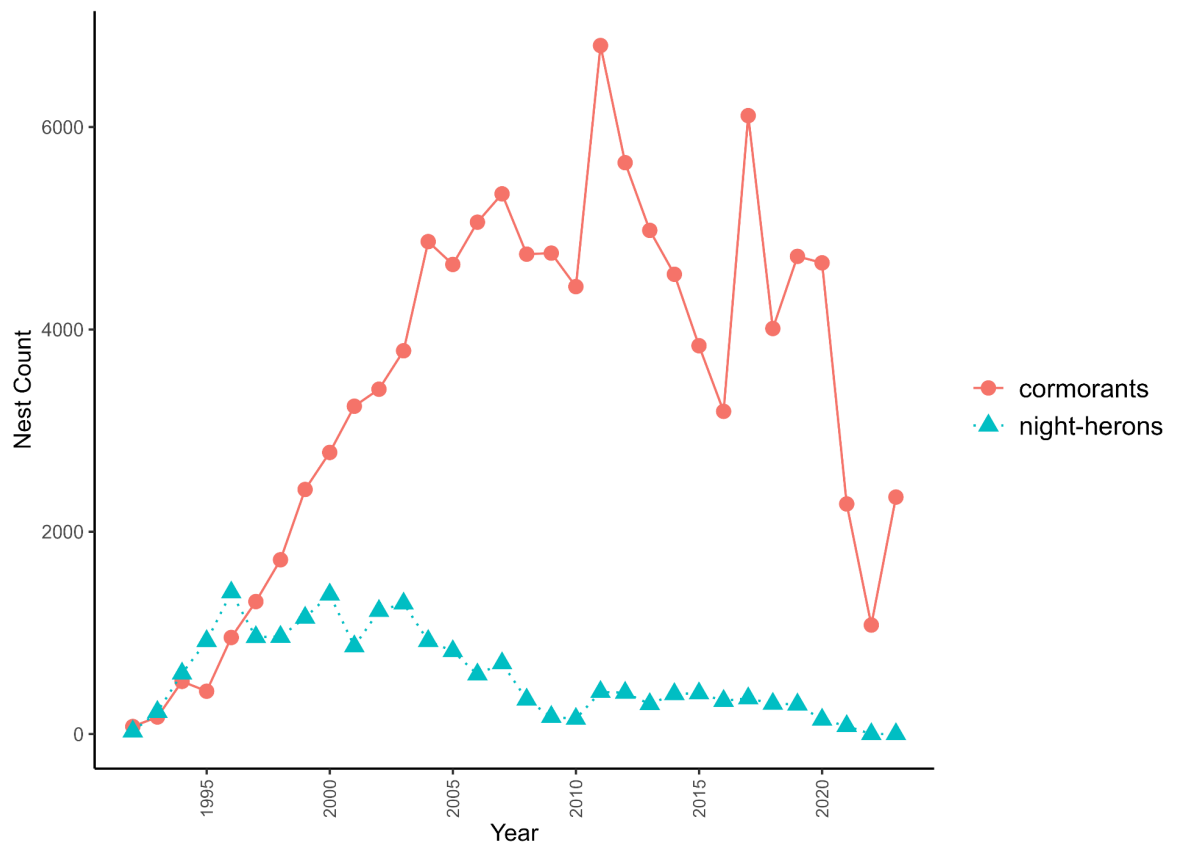


Figure 4. Population Trends of Cormorants and Night-herons at Tommy Thompson Park, Toronto, Ontario. Each point represents the total number of active nests observed during breeding season surveys from 1992-2023.

Statement of the Problem Situation⁴

Some wildlife managers and the public assume that competitive interactions between cormorants and other co-nesting waterbird species cause their decline, even though these are normal evolutionary processes. However, studies on this topic in the Great Lakes remain mostly equivocal (e.g., Cuthbert et al., 2002; McDonald et al., 2018; Skagen et al., 2001; Somers et al., 2011; Wyman et al., 2018; Wyman & Cuthbert, 2015), and the declines may be more connected to a combination of factors beyond cormorants. Given the intense management of cormorants across North America (see U.S Fish and Wildlife Service,, 2020; Wires, 2015), it is important to understand and document the interspecific interactions that managers assume to be occurring.

Research Hypothesis

Population levels of night-herons in TTP from 1992 to 2023 may have been influenced by multiple ecological factors such as: 1) night-heron-specific nest density; 2) cormorant-specific nest density; 3) cormorant nest numbers (i.e., positive colony growth); 4) nest usurpations of night-heron nests by cormorants; 5) night-heron nest success; 6) night-heron colony proximity to trails; and 7) cormorant management interventions (active nest removal with deterrence, and nighttime deterrence during the breeding season; see McDonald et al., 2018.)

Based on Wyman et al. (2018) we predicted that night-herons' nest numbers declined with an increase in cormorant nest numbers, nest density and associated cormorant management during the breeding season. A secondary effect was also predicted in that night-herons moved to areas (i.e., along trails) which increased nest failure due to raccoon (*Procyon lotor*) predation. TTP is linked to the city of Toronto by these linear features, which may provide a route for raccoons into the park.

⁴ Some material is repeated from the Introduction section.

Significance of the Study

Understanding the mechanisms driving population declines of co-nesting colonial waterbirds is critical to making informed management decisions to preserve species within a protected area. Cormorants are often heavily managed with lethal methods to control populations as concerns continue over competition between piscivorous cormorants on fisheries, impacts of guano on vegetation, and potential impacts on other species that nest in proximity to cormorant colonies (U.S Fish and Wildlife Service, 2020; Weseloh et al., 2002; Wires, 2014). Historical records suggest that cormorant populations were often much higher than what currently exists in North America (Wires & Cuthbert, 2006), and so this assumption may be based on human perception conflicts (Wires, 2015).

TTP managers have collected data annually on waterbird nest numbers and locations since cormorants arrived at the park in 1990 (see Jarvie et al., 1997; McDonald et al., 2018). This dataset is unique in waterbird management due to the extensive time frame involved- it now spans 31 years and shows the spatial dynamics of expansion of cormorants and the contraction of night-herons, though cormorant numbers have peaked and now declined. (See Figure 4; Figure 5a-5m; TRCA unpublished data). There's also some indication of a relationship between the expansion of cormorant nesting areas and the recession of night-heron nesting areas at shared colony sites in TTP (Jarvie et al., 1997).



5a. Night-herons, 1992-1993



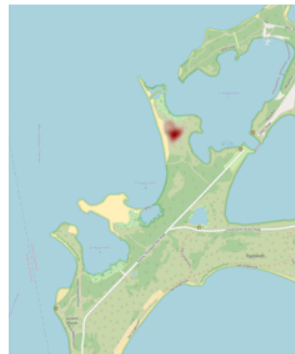
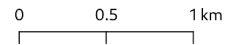
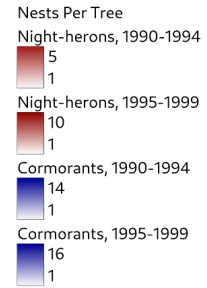
5b. Cormorants, 1992-1994



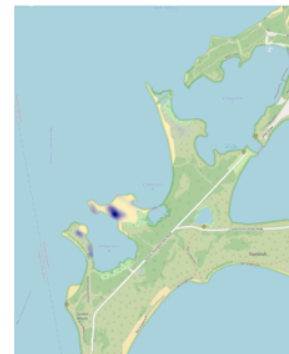
5c. Night-herons, 1995-1999



5d. Cormorants, 1995-1999



5e. Night-herons, 2000-2004



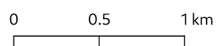
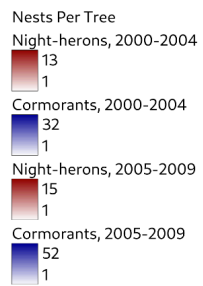
5f. Cormorants, 2000-2004



5g. Night-herons, 2005-2009

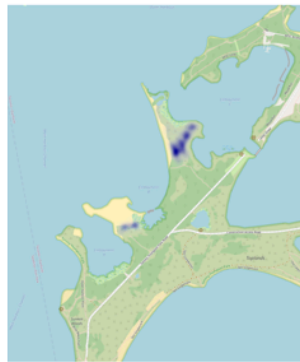


5h. Cormorants, 2005-2009





5i. Night-herons, 2010-2014



5j. Cormorants, 2010-2014

Nests Per Tree
Night-herons, 2010-2014
9
1

Cormorants, 2010-2014
96
1

Night-herons, 2015-2019
9
1

Cormorants, 2015-2019
89
1

0 0.5 1 km



5k. Night-herons, 2015-2019



5l. Cormorants, 2015-2019



5m. Night-herons, 2020-2023



5n. Cormorants, 2020-2023

Nests Per Tree
Night-herons, 2020-2023
7
1

Cormorants, 2020-2023
46
1

Figure 5a-5m. Nest locations and density of black-crowned night-herons and double-crested cormorants from 1992-2023, in 5-year time blocks, at Tommy Thompson Park, Toronto, Ontario.

Methods

Study Area

Located in Toronto, Ontario, TTP is a designated Key Biodiversity Area and Environmentally Significant Area (*About – Tommy Thompson Park*, 2020). An artificially-constructed peninsula built of brick, rubble, and dredged sand, the park juts five kilometres into Lake Ontario. Construction began in the 1950s, originally intended for “port-related activity”, but evolved through the 1970s and on into the important urban wilderness park it is today (*About – Tommy Thompson Park*, 2020). The park provides habitat for many species of migratory birds, with over 300 species documented (*About – Tommy Thompson Park*, 2020).

TTP comprises four peninsulas and multiple diverse habitats that have been built to enhance ongoing conservation and habitat restoration efforts including coastal wetlands and sheltered embayments (Figure 3). Extensive bird monitoring programs and habitat creation projects have been developed by TRCA in partnership with researchers and experts, and data collection is ongoing for migratory patterns, species diversity, and population dynamics (*About – Tommy Thompson Park*, 2020).

Nest Count Data

Annual cormorant colony monitoring began just after cormorants first started nesting in the park in 1990, with a focus on collecting the number and location of cormorant nests (i.e., colony size; see (Jarvie et al., 1997; Rosenberger, 2015). Tree nests were counted and tagged for

geo-referencing once per year at peak colony breeding sometime from late May to late June (McDonald et al., 2018). While there are earlier nest count estimates for night-herons, monitoring began the following year in 1993 after potential impacts by cormorants were suspected (Jarvie et al., 1997). Population counts of tree-nesting cormorants and night-herons from 1992 to 2023 were used for multiple datasets for this analysis (TRCA, personal communication, 2022).

Between 1992 and 2023, trees that contained cormorants or night-heron nests were tagged with an identifying number, and coordinates were recorded for each unique tree identifier. The tree tag program had challenges: 1) tags became lost or illegible and trees were given new identifiers; and 2) duplication of identifying numbers occurred when trees were tagged with pre-existing numbers, leading to complications in tracking locations over time. For this analysis, data that contained trees with the same tag number but distinct coordinates were given unique identification numbers.

Response Variable

Following Wyman et al. (2018) and Guillaumet et al. (2014), our study used a colony growth index for night-herons as the response variable to analyze what may have impacted night-heron population numbers in the park between 1992 to 2023. Colony growth index was calculated as

$$GrowthIndex_s = \frac{N_s - N_{s-1}}{\max(N_s, N_{s-1})},$$

where N_s and N_{s-1} represent nest abundance in annual survey s and previous annual survey $s-1$ respectively, and where $\max(N_s, N_{s-1})$ indicates that the larger of the values N_s and N_{s-1} should

be used here. With this definition, colony growth index takes values from -1 to 1, where -1 indicates colony abandonment and 1 indicates colonization. Values between -1 and 0 indicate declining nest abundance, and values between 0 and 1 indicate increasing nest abundance (Wyman et al., 2018). Colony growth index was calculated and used as the response variable to indicate where sites may have been abandoned or newly colonized between annual surveys of nest counts as the colony shifted over time (Guillaumet et al., 2014; Wyman et al., 2018; Figure 6).

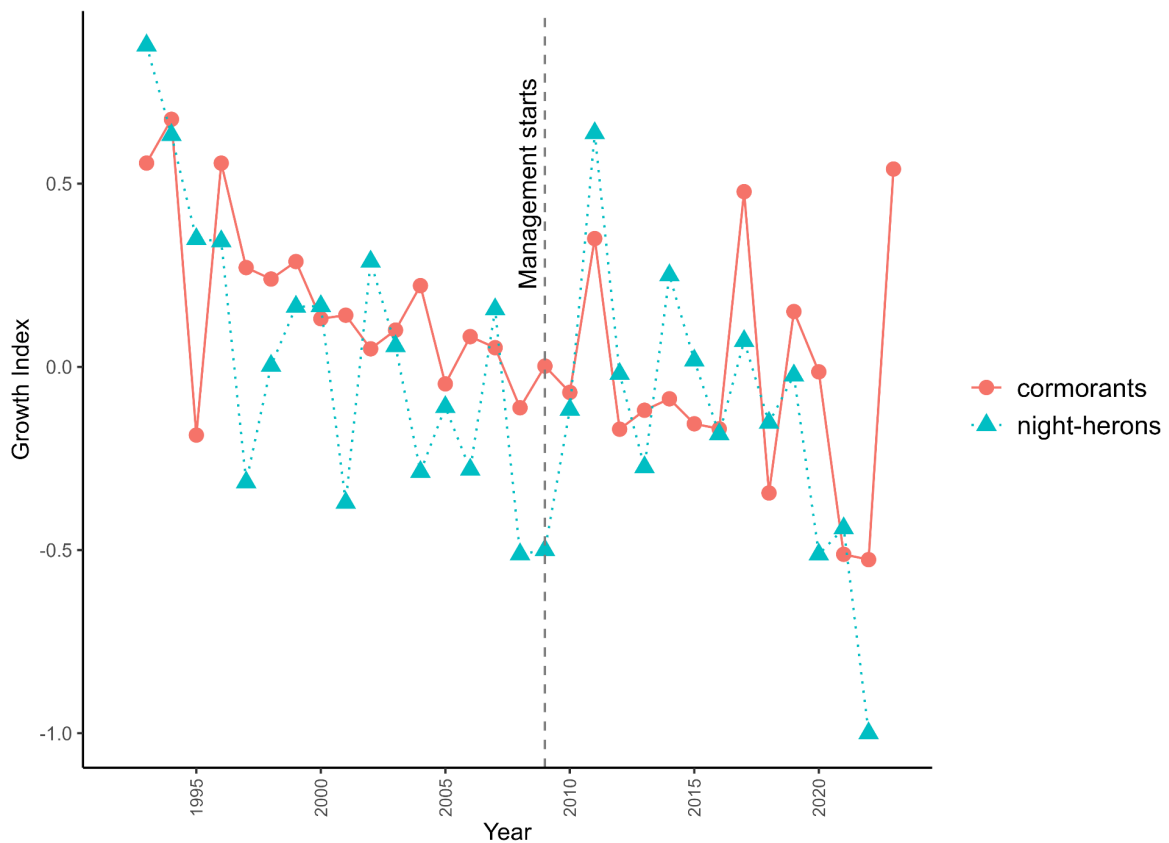


Figure 6. Night-heron and cormorant growth indices with the start of management activities indicated. Growth indices range from 1 to -1, where values between -1 and 0

indicate declining nest abundance and values between 0 and 1 indicate increasing nest abundance.

Model Covariates

Model covariates were chosen in relation to cormorant abundance (i.e., annual nest counts), nest locations, and management, as well as night-heron abundance (such as nest density and nest success), while accounting for possible predation impact and exposure to the public or other disturbances through proximity to trails. Each covariate is explained below.

Nest Density. From the geolocated nest data collected between 1992 - 2023, we calculated nest density values for night-herons and cormorants separately. Both values were used as model covariates to examine possible patterns in night-herons clustering together or when clustering in proximity with cormorants. Nest density was calculated using Moran's I spatial autocorrelation, resulting in values between 0 and 1 where 0 indicates dispersal and 1 indicates clustering patterns (Haining, 2001).

Black-crowned Night-heron Nest Success. From 2009 to 2021 (except 2020), we annually followed a sample of night-heron nests from May to August. To assess nest success, nests were visually checked with binoculars from the ground weekly until there were no sample nests left to monitor. At each weekly observation we recorded the state of the nest (partial, full, intact, falling), adult presence and posture (standing on nest, standing near nest, sitting), and chick presence, number of chicks and notes on chick development. We used the Mayfield, (1975) method – in which incubation is inferred when we first observed a bird sitting while it was incubating – to estimate total nest survival probability and nest success (the proportion of nests which fledged at least one chick observed; Erwin & Custer, 1982). As the age of nest content was unknown (i.e., lay date unknown), we estimated chick age at last observation by subtracting

the average length of incubation (24 days; Hothem et al., 2010) out of the total number of days the nest was observed. A nest was identified as successful if chicks were observed (or estimated in age) in the nest for 35 days or longer (Hothem et al., 2010). The resulting value is between 0 and 1, indicating a percent per year of successful nests.

Raccoon Predation. In seven study years (2009, 2010, 2011, 2014, 2015, 2016, 2017), we were able to estimate the raccoon predation on night-heron nests using foil wrapped around trees (Gentile, 2022). The values included are between 0 and 1 representing the percentage of nests predated upon by raccoons annually out of total nests followed. Numbers are approximate as predation also occurred outside of direct observation.

Cormorant Usurpation of Night-heron Nests. While collecting nest success data from 2008-2021 for night-herons, we also tracked whether a nest was usurped by a cormorant. A nest was considered usurped if a cormorant was observed in a nest which had a night-heron observed in the week prior. Every year some night-heron nests found in the nest building stage “failed” prior to initiating incubation; these nests were not included in the nest usurpation estimates even though some nests were usurped in the pre-laying stage. Cormorant usurpations of night-heron nests were included from annual nest observations as a number between 0 and 1 representing a percent per year of nests usurped annually out of total nests followed.

Night-heron Proximity to Trails. Motorized vehicles are not permitted in Tommy Thompson Park and main paved trails throughout the park are used primarily by park vehicles and visitors. Proximity to roads and trails, and the human disturbances that are associated with them, has been shown to have significant impacts on colonial waterbirds (see Rodgers & Smith, 1995; Carney & Sydeman, 1999), and despite policies in place to minimize wildlife impacts such as banning of pets and audio speakers, wildlife disturbances due to public park use are likely.

Carney & Sydeman (1999) reviewed multiple studies of the effect of human disturbances on nesting colonial waterbirds and found that the effects varied widely among species. With no specific recommendation for night-herons available, it was generally recommended that buffer zones of 100-250 meters alongside roads for most species were best to minimize disturbance impacts (Carney & Sydeman, 1999). Trail-specific recommendations were not available. Linear features may be used as travel routes or access to the park by predators, such as raccoons, as well (DeMars & Boutin, 2018).

To account for night-herons' colony disturbances due to proximity to trails, trails throughout the park were estimated to be an average single-lane road width of 9 metres. We set a buffer of 100 metres around trail features used by visitors and TRCA vehicles throughout the park and exported an annual count of night-heron nests for inclusion in the model. Trail proximity counts were included in the model as a value between 0 and 1 representing percentage of nests annually out of total nests observed that year in proximity to a trail.

Cormorant Management. Management activities for the cormorant colony began in 2009 and deterrence activities were divided into three primary activities. Winter nest removal occurred before the breeding season (November to March) from 2010 onwards to discourage tree nesting (McDonald et al., 2018; TRCA unpublished data). Deterrence activities with active nest removal occurred during the pre-nesting phase in April from 2009 onwards (except in 2020). Night-time deterrence activities occurred from two to nineteen times annually from 2009 to 2023, except in 2012 due to the presence of night-herons in proximity to the colony (and in 2020). Night-time deterrence was integrated into regular management activities in 2016 (dawn to dusk deterrence). This took place during peak nesting (typically the last week of April or first week of May, to the first week of June)- managed adaptively based on cormorant nest building behaviour (A.

Chreston, personal communication, December 22, 2024; McDonald et al., 2018; TRCA unpublished data).

Only one variable was included in the model to account for management that occurred during the breeding season. Management for the colony is included as a binary indicator, with 0 indicating no management activity occurred and 1 to indicate that management activity occurred for that calendar year. Further data to quantify management effects (such as number of nests removed, or number of days deterrence occurred) is largely unavailable and so was omitted from model inclusion.

Usurpation of Night-heron Nests by Cormorants. Usurpation of night-heron nests by cormorants was included in the model from observational data between 2009 and 2020. The values included are a value between 0 and 1 representing the percentage of nests usurped annually out of total nests followed.

Statistical Analysis

We used linear mixed-effects models to relate cormorant abundance and management to night-heron covariates. Analysis was conducted using Bayesian inference and implemented through the MCMCglmm package in R version 4.2.2 (R Core Team, 2024). Three candidate models were constructed to compare potential parameters for model fit, evaluated with Deviance Information Criterion (DIC; Table 1), a statistical measure that balances model complexity with goodness of fit, where lower values indicate models that explain observed data more efficiently (Spiegelhalter et al., 2002). Model one included fixed effects of night-heron nest density, cormorant nest density, night-heron nest success, cormorant growth index, night-heron trail proximity, cormorant usurpation, and management. Model two included fixed effects of night-heron nest density, cormorant nest density, cormorant growth index, night-heron trail

proximity, cormorant usurpation, raccoon predation, and management. Model three, selected as that with best fit, included fixed effects for night-heron nest density, cormorant nest density, cormorant growth index, night-heron trail proximity, and management during the breeding season.

Table 1. Covariates used for each model. ‘BCNH’ indicates Black-crowned Night-herons and ‘DCCO’ indicates Double-crested Cormorants.

Model 1	Model 2	Model 3
Intercept	Intercept	Intercept
BCNH Nest Density	BCNH Nest Density	BCNH Nest Density
DCCO Nest Density	DCCO Nest Density	DCCO Nest Density
BCNH Nest Success	DCCO Growth Index	DCCO Growth Index
DCCO Growth Index	BCNH Road Proximity	BCNH Road Proximity
BCNH Road Proximity	Usurpation	Management
Usurpation	Raccoon Predation	
Management	Management	

Model 3 was constructed as follows. Models 1 and 2 were constructed similarly with appropriate combinations of covariates included (Table 1).

$$\text{night-heron growth index}_i \sim \text{Normal}(\mu_i, \sigma^2)$$

$$\mu_i = \beta_0 + \beta_1 * \text{night-heron nest density}_i + \beta_2 * \text{cormorant nest density}_i + \beta_3 * \text{cormorant growth index}_i + \beta_4 * \text{trail proximity}_i + \beta_5 * \text{management}_i + \alpha_{\text{year}[year_i]}$$

$$\alpha_{year}[year_i] \sim Normal(0, \sigma^2_{year})$$

Where i indexes the observations, β_0 is the intercept, β_1 through β_5 represent the corresponding fixed effects coefficients, and $\alpha_{year}[year_i]$ represents the random effect for year. The random effect for year is assumed to follow a normal distribution with mean 0 and variance σ^2_{year} .

Covariates for each test model were chosen by combining relationships while seeking to avoid multicollinearity by not including redundant variables that capture similar relationships or information, which may result in overfitting of the model. Numerical covariates were scaled. Due to significant missing data (such as reduced available timespan of observational data) depending on the covariate, models were fit using Bayesian approach to compensate for additional uncertainty and missing values handled through multiple imputation. Percentages of missing data range from 78.9% percent (for raccoon predation observations) to 6.1% for growth indices, with three variables having missing data rates of >60% (raccoon predation, night-heron nest success, and usurpation observations).

We reconstructed missing data through Bayesian imputation using informative normal prior distributions for continuous data, based on means and standard deviations of observed data, and truncated at zero for nest densities and growth indices. A Bernoulli distribution was used to impute the binary management indicator. Weakly informative normal priors were used for fixed effects and parameter expanded priors for random effects. Using Bayesian imputation allows for uncertainty in missing data while making use of available data.

We ran three simultaneous chains for 50,000 iterations as determined by the number of iterations required to achieve Monte Carlo standard of <2% of posterior distribution standard deviation and R-hat values <1.1. The R-hat statistic measures chain convergence, with values

close to 1 indicating that chains have converged to the same posterior distribution (Gelman & Rubin, 1992). Convergence was visually assessed with trace plot inspection and effective sample size examination.

Parameter estimates were presented as posterior means, with 95% credible intervals calculated. Model fit was evaluated using Bayesian p-values following King (2010). A discrepancy function, based on the sum of the square residuals, was calculated for both the observed data and replicated data generated from the model to compare observed night-heron growth indices to those predicted by the model. Bayesian p-values (pMCMC) range from 0 to 1 (King, 2010). The resulting p-values were evaluated, with values moderately close to 0.5 indicating good model fit (meaning the fit of the model to the observed data is comparable to the fit of the model to data simulated from the model itself.). Extreme p-values (closer to 0 or 1) indicate poor fit.

Results

Model three had the least number of parameters and achieved the best DIC score, likely avoiding overfitting while capturing the most important relationships in the data (Burnham & Anderson, 2004; see Table 2). Additional variables included in the other models, such as nest usurpation and raccoon predation, did not substantially improve model performance, indicating these variables may be less crucial in explaining variation in night-heron colony growth. Selection of model three was further supported by its significant parameter estimates, suggesting important interspecific dynamics in this mixed-species colony.

Table 2. Estimated parameters of Black-crowned Night-heron (BCNH) colony growth models examining the relationship with Double-crested Cormorant (DCCO) abundance.

Values represent posterior means and 95% credible intervals for the 3 models tested.

Significant effects are indicated by credible intervals that do not overlap zero. Model 3 was selected as that with best fit (DIC -29.934), indicating that the model balances complexity with explanation of observed data more efficiently (Spiegelhalter et al., 2002).

Model 1 DIC Score: -13.593, Bayesian P-value: 0.313

Parameter	Mean	Upper Credible Interval	Lower Credible Interval	pMCMC
Intercept	-0.108	-0.352	0.160	0.392
BCNH Nest Density	0.334	0.054	0.635	0.025
DCCO Nest Density	-0.017	-0.307	0.272	0.911
BCNH Nest Success	0.574	0.243	0.912	0.002
DCCO Growth Index	0.745	0.384	1.065	0.001
BCNH Trail Proximity	0.241	-0.090	0.573	0.148
Usurpation	-0.218	-0.572	0.108	0.193
Management	0.051	-0.245	0.372	0.731

Model 2 DIC Score: -3.117, Bayesian P-value 0.438

Parameter	Mean	Upper Credible Interval	Lower Credible Interval	pMCMC
Intercept	-0.061	-0.373	0.260	0.688
BCNH Nest Density	0.260	-0.111	0.589	0.150
DCCO Nest Density	0.046	-0.320	0.415	0.804
DCCO Growth Index	0.787	0.355	1.220	0.001
BCNH Trail Proximity	0.001	-0.355	0.357	0.999
Usurpation	-0.232	-0.652	0.187	0.264
Raccoon Predation	-0.097	-0.440	0.290	0.600
Management	0.164	-0.186	0.544	0.356

Model 3 DIC Score: -29.934, Bayesian P-value: 0.438

Parameter	Mean	Upper Credible Interval	Lower Credible Interval	pMCMC
Intercept	-0.051	-0.354	0.268	0.745
BCNH Nest Density	0.187	-0.131	0.530	0.259
DCCO Nest Density	0.110	-0.229	0.458	0.514

DCCO Growth Index	0.623	0.274	0.957	0.000
BCNH Trail Proximity	-0.073	-0.422	0.275	0.660
Management	0.180	-0.185	0.560	0.326

Results showed a positive relationship between cormorant growth index and night-heron growth index (posterior mean = 0.623, 95% credible interval [0.274, 0.957]). This indicates that when cormorant populations grew, heron populations tended to grow as well. Cormorant growth consistently shows a positive relationship with night-heron growth across all models tested. Nest density of night-herons (posterior mean = 0.187, 95% credible interval = [-0.131, 0.530]), nest density of cormorants (posterior mean = 0.110, 95% credible interval = [-0.229, 0.458]), night-heron proximity to trails (posterior mean = -0.073, 95% credible interval = [-0.422, 0.275]), and management activities (posterior mean = 0.180, 95% credible interval = [-0.185, 0.560]) have wide credible intervals crossing zero and are not statistically significant, suggesting substantial uncertainty in the effects of these variables on night-heron growth indices. This may be influenced by small sample sizes, leading to uncertainty in parameter estimates, high variability in the response variable or predictor variables, and high variability naturally present in complex ecosystems due to unmeasured interactions or other factors.

Management activities during the breeding season show a slight positive effect on night-heron growth indices, (posterior mean = 0.180) but are not statistically significant (pMCMC = 0.326). The wide credible interval [-0.185, 0.560] suggests high uncertainty about this impact.

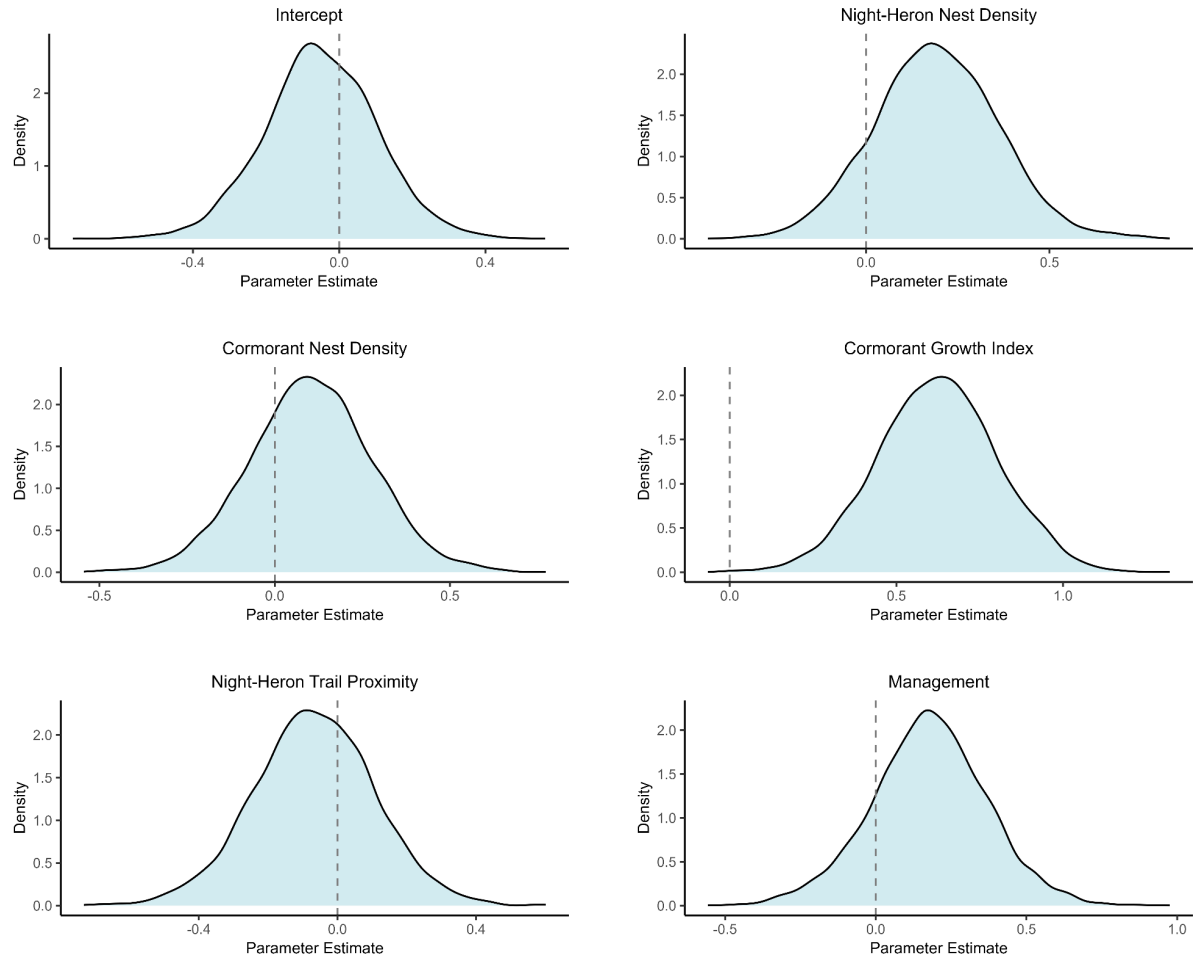


Figure 7. Estimated posterior density distributions of parameter estimates from Model 3 examining factors affecting night-heron growth index. Vertical dashed lines represent zero (no effect) Distributions that do not substantially overlap zero indicate stronger evidence of an effect. The width of each distribution indicates the uncertainty in the parameter estimate.

Discussion

Waterbirds nesting in mixed-species colonies may compete for resources or encounter aggressive interspecies interactions, favouring the success of one species over another or causing a species to abandon an area (see Jarvie et al., 1997; Gorski & Pajkert, 1997; Varela et al., 2007;

Ellis & Good, 2006; Somers et al., 2011). The strong positive relationship found between cormorant and night-heron population growth was contrary to common assumptions. Night-herons may benefit from the presence of cormorants, as seen between grey herons foraging on regurgitated fish from cormorants (Wojczulanis et al., 2005). This positive relationship could indicate a mutual benefit of night-herons and cormorants from habitat features or environmental conditions at Tommy Thompson Park, or night-herons benefiting from resources due to cormorant proximity.

Lack of significant effects of cormorant nest density on night-heron population growth challenges the expectation that proximity between night-herons and cormorants increases interspecific competition, and that crowding directly influences colony dynamics (see also Skagen et al., 2001; Somers et al, 2011; Somers et al, 2007, Taylor et al, 2011, Wyman & Cuthbert, 2011). However, our data had wide credible intervals indicating uncertainty, so density-dependent effects cannot be ruled out. Wyman et al. (2018) found that night-herons had negative associations with cormorant abundance, though Skagen et al. (2001) found that great blue heron declines near a cormorant colony were caused by a combination of human disturbance, changes in environmental conditions, and competition by cormorants. Cuthbert et al. (2002) found that cormorant presence did not cause night-heron or great blue heron declines except under special circumstances.

Previous studies of cormorant and night-heron dynamics found a relationship between expanding nest areas of cormorants and the receding nest areas of night-herons at two peninsulas in TTP (Jarvie et al., 1997). However, Rosenberger (2015) found through spatial analysis and focal nest observations that cormorants seemed to play a role in the decline of night-herons at TTP through indirect effects only on one peninsula, with negligible impacts on the second

peninsula. Our study did not examine peninsulas individually, so further research may be needed to determine if effects differ based on location.

Management activities during the breeding season show a slight positive effect on night-heron growth indices, but are not statistically significant. The wide credible interval suggests high uncertainty about this impact. This finding differs from Wyman et al. (2018), who found that night-herons had negative associations with increasing management intensity, with more management visits associated with greater night-heron reductions. This difference may be due to several factors. First, night-heron nest numbers at our study site started to decline before the commencement of management actions in 2009 (Figure 6), suggesting other drivers of population change. Second, while Wyman et al. (2018) found that cormorant presence reduced night-heron growth index, our study found a positive relationship between the two species' growth. High uncertainty in this estimate indicates that further refinement of the model, or further parameters or refinement of data, could be needed. Cuthbert et al. (2002)'s work supports the complexity of these relationships, finding that night-heron declines were only associated with cormorant presence in certain instances, with declines often driven by other factors (such as management practices, successional vegetation changes, storms, and high water levels).

Linear features have been shown to increase predator-prey interactions, leading to potential increases in predator movement into and within prey refugia and increased predation (DeMars & Boutin, 2017). Proximity of night-heron nests to trails within TTP did not show clear effects, suggesting that this source of human disturbance and raccoon predation via trail access may not be a key driver of night-heron colony dynamics. We hypothesized that night-heron proximity to trails would increase nest failure due to access by raccoons, which is not indicated

by this result. It is possible that refinement of buffer zones around trails, possibly based on trail use frequency, could provide more refinement for the analysis of human disturbance.

Random year effects show substantial temporal variation, emphasizing the importance of long-term monitoring of colonies in order to understand dynamics. Populations may be influenced by varying factors across years that are not accounted for in this study (such as weather patterns, resource availability, and ecosystem changes (Clutton-Brock & Sheldon, 2010)).

It is important to highlight the uniqueness of the data provided by TRCA. The conservation authority has collected data since cormorants arrived at the park in 1992, resulting in a dataset of more than 30 years at one of the largest cormorant colonies in North America. Similar studies on colonial waterbirds have shorter timeframes or less years of data, with most including between four and eight years of census data and less of observational data (though sometimes over a 40 year timeframe) (see Cuthbert et al, 2002; Shieldcastle & Martin, 1997; Skagen et al., 2001, Somers et al., 2011; Wojczulanis et al., 2015; Wyman & Cuthbert, 2015; and Wyman et al., 2018). TRCA has continued to recognize the role of cormorants in ecosystem health in the Great Lakes region, and its approaches to long-term monitoring and adaptive, spatially-focused management have sought to balance ecological, scientific, and recreational values within the park with the existence of a healthy colony (McDonald et al., 2018). Longer-term monitoring like TRCA has undertaken, and the continuation of large datasets, are critical to increasing understanding of ecological complexity, documenting responses to environmental change, contributing to predictions of future impacts to biodiversity, and determining the effectiveness of management interventions (Lindenmayer et al., 2022).

While our model identified cormorant growth as a significant predictor of night-heron growth, contrary to expectations of impacts between species, wide credible intervals for most

parameters suggest that night-heron population dynamics are complex and likely influenced by interacting factors not captured in this analysis. Further research would benefit from larger sample sizes of parameters with shorter timeframes (usurpation, raccoon predation, and nest success) to reduce parameter uncertainty. Further analysis of environmental variables such as vegetation density or weather patterns, more refined measurements of human disturbance or raccoon predation, or further observations of interspecific interactions would be helpful in revealing influences on cormorant and night-heron populations not captured in this study. Further refinement of the data and model could allow the inclusion of parameters that were not in the final model, especially evidence of repeated raccoon predation and usurpation of night-heron nests, which likely explain some of the dynamics at play in this colony.

Methodological Limitations

This study uses data of nest count estimates spanning from 1992 to 2023 for cormorants and night-herons within Tommy Thompson Park in Toronto, Ontario, Canada. Included in the data are records of individually tagged trees, trees tag per nest, coordinates for the tree, tree species, and peninsula location. Tree species were not included in this study, and peninsula locations were excluded due to difficulty classifying locations for trees that lay between peninsulas. The study looks at patterns broadly across all areas of the park where nest counts were recorded to examine overall trends and impacts on night-heron nests within the park.

Data of nest success and usurpations are limited to when studies were conducted by researchers from 2009 onward until night-heron nests were no longer observed in the park in 2022. Data of nest success and usurpations were not available for either species in 2020 due to lack of personal protective equipment (PPE) availability in the early stages of the COVID-19 pandemic. Management data were included from 2009 onward when cormorant colony

management began in the park. The final year of night-heron colony growth index data is in 2021. Night-heron absence occurred in 2022. Two nests were recorded in 2023 and were not included in this analysis.

Data quality issues became a concern due to missing data over significant periods of time, depending on the dataset (see Statistical Analysis), and there were inconsistencies in data entry in collection over time due to the high volume of data collected over 31 years and variance in methods across teams. Trees that contained night-heron or cormorant nests were tagged with identifiers to record counts over time; challenges occurred when tags were lost and replaced over the years, as well as instances of duplication of numbers for tree tags that occurred.

Chapter Three: Reflection on Thesis Development and Challenges

Following the completion of the primary thesis study in *Guano Rain and Growing Pains: Co-nesting Dynamics of Double-crested Cormorants and Black-crowned Night-herons at Tommy Thompson Park*, this reflection aims to capture the complexity of the research process and outline areas for future development. The evolution of this thesis project exemplifies the dynamic nature of ecological research and the value of adaptability in scientific inquiry.

Initially conceptualized as spatial analysis of both colonies, this study intended to build upon the work of Jarvie et al. (1997) and Rosenberger (2015), examining trends of cormorants and night-herons in Tommy Thompson Park with an additional seven years of data. However, guided by the expertise of my supervisor and committee member, the project's scope expanded significantly to incorporate Bayesian inference and ecological modeling. This methodological shift was inspired by Wyman et al. 's (2018) approach, which examined potential cormorant impacts on multiple co-nesting species across North American colonies using ecological models with Bayesian inference.

The switch to Bayesian inference in ecological modeling aimed to include a more nuanced understanding of the data by capturing additional influences on night-heron populations. Data were available for additional factors that could increase understanding of cormorant-heron interactions in the park such as nest usurpation, predation, proximity of night-heron nests to roads, and management practices for the cormorant colony. Much of the data were only available for limited time frames from observational studies.

This expanded approach was driven by the hypothesis that raccoon predation or proximity to roads may have a more significant impact on night-herons than proximity to cormorant colonies. Additionally, understanding the potential effects of cormorant colonies on

co-nesting waterbirds could have important implications for wildlife management strategies within Tommy Thompson and other cormorant colonies.

This reflection section will explore the challenges encountered, lessons learned, and personal growth experienced throughout this evolving research process. It will also discuss the potential broader impacts of this study on ecological understanding and conservation practices.

This study examined the complex dynamics between cormorants and night-herons at TTP over a 31-year period from 1992-2023. Using Bayesian linear mixed-effect models, we analyzed multiple factors potentially impact night-heron colony growth, including cormorant abundance, nest densities of both species, management practices, and proximity to roads (linked to human disturbance and raccoon predation). The most relevant finding was a significant positive relationship between cormorant and night-heron growth indices, challenging common assumptions about interactions between the two species and not quite aligning with previous findings by Jarvie et al. (1997) and Rosenberger (2015). While most variables show high uncertainty in their effects, this unexpected positive association suggests that both species may respond similarly to favourable habitat conditions or other unaccounted-for impacts, and that the relationship between cormorant population increase and night-heron declines is still undetermined.

Challenges of Long-term Data Analysis

Throughout this study, data preparation emerged as the most challenging and time-consuming aspect. TRCA data spanned 31 years of nest counts for each species, with collection standards evolving over time due to multiple contributors and collection standard changes. While previous students had created databases in 2015 and 2018 (Rosenberger, 2015,

and Imran, unpublished thesis), significant challenges remained in integrating new annual counts and addressing potential data gaps.

Data collection standards varied considerably throughout the years, and methods for indicating new tree tags were inconsistent. To address this, I worked to add new tree tags to the existing database using Excel formulas to add nest counts for each species per tree tag. I implemented a search-and-add function for tags not explicitly indicated as new in TRCA records, which uncovered many more new tags than originally indicated in the datasets. I recorded replaced tree tags in a separate column, using the existing tag as a unique ID for continuity. Finally, I went through previously created databases with similar search-and-find functions for peninsula and coordinate information to increase consistency throughout the dataset.

This process revealed the complexity of maintaining data integrity across long-term ecological studies and highlighted the importance of consistent data collection and management practices.

Spatial Analysis Challenges

Preparing data for spatial analysis presented additional challenges such as locating missing tree coordinates, addressing inconsistencies in coordinate formats, converting coordinates to ensure uniformity, and resolving tree tag duplications. These challenges underscored the critical nature of standardized data collection methods in long-term ecological studies and the need for meticulous data cleaning and verification processes.

Experience with Bayesian Modeling

With little-to-no experience with Bayesian statistics and ecological modeling, developing and implementing this model presented a unique academic challenge. This process required learning Bayesian statistical fundamentals, understanding ecological modeling principles,

improving programming skills in R, and studying published ecological Bayesian models. The complexity of creating a Bayesian model involved developing an understanding of how to define the research question, specifying the model structure and comparing model parameters, choosing prior distributions, data preparation, running the model, assessing model fit and performing model checking, and interpreting results for discussion. Despite the steep learning curve, each step provided valuable insights into advanced statistical methods and their application in ecological research.

Many tools exist to assist a researcher in learning or improving their coding skills in R as well as Bayesian inference in ecological modelling; the challenge can become sorting through the myriads of resources, articles, and platforms available to find what is relevant and approachable. As Lawlor et al. (2022) highlighted, statistical and scientific programming is a valued skill in the sciences but not always a prerequisite in a natural sciences degree.

Self-learning statistical programming requires efficient use of strategies and resources in order to conquer the steep learning curve (Lawlor et al., 2022). For those choosing to follow a similar path, it is recommended to make use of free resources developed by the R community. As an open-source software, there are many books and resources available for learning R (see Wickham et al., 2017, Lawlor et al., 2022) and I recommend choosing resources that enable the student to practice in R with practice problems relevant to their desired learning outcome.

Courses developed to learn both ecological modeling and R such as Coding Club (Daskalova et al.) enable students to learn the foundations of R with test projects relevant to environmental science and ecological modeling.

Lessons Learned and Future Directions

Completion of this thesis has provided insight for future studies such as the importance of a strong foundation in statistical methods before undertaking complex modeling projects, the value of efficient data management and preparation techniques, and the benefits of leveraging existing models and published research when developing new approaches. For future studies, I would verify data cleaning methods and model requirements earlier in the process, focus on understanding the conceptual aspects of modeling rather than getting bogged down in programming details, and allocate more time for data preparation and quality assurance.

This experience has opened new avenues for potential career paths and further academic pursuits, possibly including doctoral studies. The power of Bayesian inference in ecological modeling has sparked a continued interest in learning and applying these methods to enhance our understanding of complex ecological systems.

While not a new methodology, ecological modeling using Bayesian inference provides a more nuanced and complex option for statistical analysis that may capture prior knowledge and uncertainty of the ecological processes being studied. Future iterations of this study could look at incorporating possible population impacts such as undergrowth density, which was omitted from this study due to time constraints. This research has several important implications for colonial waterbird management and conservation. First, the positive association between cormorant and night-heron growth challenges the common assumption that cormorant population growth likely harms other colonial waterbirds. This finding suggests that management decisions based on assumed negative impacts of cormorants on co-nesting species should be examined.

Second, the high uncertainty in most parameter estimates highlights the complexity of colonial waterbird dynamics and the need for consideration of multiple factors in management decisions. The weak negative association between management activities and night-heron

growth, though not statistically significant, suggest that management practices may need refinement to support co-nesting species.

Third, this study demonstrates the value of long-term ecological monitoring and data collection, even when collection methods change over time. The 31-year-dataset, despite its challenges, provided insights that shorter-term studies may not illuminate. This underscores the importance of maintaining long-term monitoring programs at cormorant colonies.

Finally, the successful application of Bayesian methods (following Wyman et al., 2018) to handle missing data and uncertainty create a framework for future studies dealing with similar ecological datasets, especially colonial waterbird populations where data collection may be irregular or incomplete.

Conclusion

This thesis investigated complex interspecific relationships and co-nesting dynamics between double-crested cormorants and black-crowned night-herons in Tommy Thompson Park, Toronto, Ontario. Cormorant populations have rebounded since near extirpation due to pesticides in the Great Lakes region in the 1970s, and Tommy Thompson Park is home to one of the largest non-lethally managed colonies (Hatch, 1995; Weseloh et al., 2002). The colony has grown from 6 nests to over 10,000 annual nests since 1992 and night-heron populations have declined significantly since cormorant arrival, to complete absence in 2022 (TRCA unpublished data).

The use of Bayesian linear mixed-effects models allowed analysis of impacts to night-heron growth indices while incorporating multiple ecological factors and cormorant colony management, following Wyman et al. (2018) analysis of co-nester impacts by cormorant colonies. Using Bayesian inference assisted in addressing challenges with missing data (King, 2010). Limitations existed in the study due to uncertainty in parameter estimates likely due to small sample sizes, high variability in response and predictor variables, or other unaccounted for factors in the ecosystem yet to be determined. Working with long-term data collection led to potential data quality issues such as missing or limited data over the 31 years included in the study, as well as evolving data collection practices over time and the need for extensive data cleaning.

Key findings indicated strong positive associations between cormorant and night-heron population growth indices, suggesting both species may be responding favourably to an unaccounted-for factor such as habitat conditions, rather than existing in a purely competitive relationship (Somers et al., 2011; Wyman et al., 2018). Most other variables, including nest densities, proximity to roads, and management activities, showed high uncertainty in their effect

on night-heron growth. The weak positive effect of cormorant management practices on night-heron growth indices, while not statistically significant, differs with previous studies suggesting potential negative impacts of management activities on co-nesting species (see Carney & Sydeman, 1999; Wyman et al, 2018).

This study underscores the complexity of co-nesting colonial waterbird dynamics. The relationship between cormorants and night-herons may be more subtle than originally thought, with both competitive and facilitative interactions potentially at play (Somers et al., 2011; Cuthbert et al., 2002). The positive effects of cormorant management practices on night-heron growth indices suggest that current methods of management of the colony may benefit night-heron populations, though high uncertainty in these estimates prevents definitive conclusions and previous studies have indicated potential negative impacts of cormorant management on co-nesting night-herons (see also Cuthbert et al., 2002; Wyman et al., 2018). The positive association between night-heron and cormorant growth suggests that there are complex dynamics between the two species that may need to be considered in management approaches (Somers et al., 2011; Skagen et al., 2001).

Further research could seek to include more thorough inclusion of management data or further observations, as well as larger sample sizes, to reduce uncertainty in parameter estimates. Satellite imagery could be used to analyze potential impact of understory vegetation density over time. Finally, more refinement of the data may be needed, such as inclusion of peninsulas to look for smaller scale trends within the park.

In conclusion, this thesis underscores the intricate relationships between co-nesting species in mixed species colonies, specifically of cormorants and night-herons, as well as the challenges of long-term ecological research. While some expected competitive effects were

observed, unexpected positive associations and minimal impacts of management practices were also found. These results highlight the need for nuanced, evidence-based approaches to managing mixed-species waterbird colonies (Wires, 2015) and the value of long-term, consistent ecological monitoring.

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