Analysis of double-crested cormorant nest spatial patterns in single and mixed-species colonies and their effect on cormorant behaviour and on black-crowned night heron spatial patterns

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Abstract

Double-crested cormorants (*Phalacrocorax auritus*) are managed because they eat fish, transform habitat and can affect other waterbirds. Conversely, cormorants have been highly successful in North America since the 1970s due to increased food supply and their adaptability, although other factors may be important. I researched cormorants at Tommy Thompson Park, Ontario, and tested 1) whether tree-nesting cormorants nesting with black-crowned night herons (*Nycticorax nycticorax*) decreased heron population through direct or indirect effects and 2) whether ground-nesting cormorants changed their behaviours due to nest density or position and whether there was a behavioural trade-off that affected fledging success. Cormorant variables were correlated with heron declines due to indirect effects in some areas. Increased density was related to lower aggression, but there were no trade-offs between the behaviours. My research illustrates the different behaviour and spatial patterns for cormorants in single and mixed-species colonies and in ground versus tree nesting colonies.

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Table of Contents

Chapter 3 - Analysis of behaviour trade-offs and their relationship to density, position and fledging success in ground-nesting double-crested cormorants

List of Tables

The effect of double-crested cormorants on the distribution and behaviour of breeding colonies of black-crowned night herons

Analysis of behaviour trade-offs and their relationship to density, position and fledging success in ground-nesting double-crested cormorants

List of Figures

The effect of double-crested cormorants on the distribution and behaviour of breeding colonies of black-crowned night herons

Analysis of behaviour trade-offs and their relationship to density, position and fledging success in ground-nesting double-crested cormorants

General Introduction

Coloniality: Evolution and dynamics

Despite being researched for more than 60 years, there is no consensus on why species nest in colonies (Coulson 1968; Danchin and Wagner 1997; Rolland et al. 1998; Racine et al. 2012). Colonial breeding is found in many taxa, including reptiles and mammals (Fritz and Trillmich 1984; Baldi et al. 1996). In birds, many different species form colonies, such as cliff swallows (*Petrochelidon pyrrhonota*), European bee-eaters (*Merops apiaster*) and rock sparrows (*Petronia petronia),* but it is predominantly a strategy in waterbirds, with approximately 98% breeding in this way (Brown and Brown 1987; Rolland et al. 1998; Hoi and Hoi 2002; Valera et al. 2003). It is likely that colonial breeding evolved at least 21 times independently and many possible explanations exist as to why it is so prevalent (Rolland et al. 1998). It may have evolved as a form of predator protection, since in colonies, there are more birds available to mob predators and more birds present to detect their presence (Brown and Brown 1987; Hernández-Matías et al. 2003; Varela et al. 2007). Birds breed relatively synchronously in colonies as well, so they can swamp predators through a dilution effect so that more young will survive (Hötker 2000; Jovani and Grimm 2008). The information centre hypothesis states that colonies may have evolved as a method of information exchange to facilitate finding food or because they facilitated the ability of birds to learn valuable skills, such as how to raise young successfully, especially since many colonial species delay reproduction (Ward and Zahavi 1973; Schjørring et al. 1999). The formation of breeding colonies may have been a by-product of other forms of bird behaviour. Birds may end up aggregating in certain areas because they use the presence of another individual to gage the quality of an area (habitat selection hypothesis) or to facilitate finding a mate (hidden lek hypothesis) (Wagner et al. 2000). Some of these hypotheses, such as the information centre hypothesis, are refuted in studies on specific species, making it difficult to determine whether any of them are valid, so it is possible that some factors affect some species but not others (Rolland et al. 1998; Varela et al. 2007; Racine et al. 2012). Whatever the reason colonies may have evolved, their continued prevalence means that they are a successful way for birds to raise young (Danchin and Wagner 1997).

Coloniality evolved due to the advantages that it confers on breeding birds. However, there are many negative aspects to living in colonies and in fact, the benefits that colonies confer can also have negative side-effects (Danchin and Wagner 1997). Colonial breeders benefit from nesting in large aggregations to decrease the risk of predation and find mates (reviewed in Clode 1993). However, the large, dense concentrations of birds in colonies can promote the transfer of disease and parasites (Valera et al. 2003). Colonies are more conspicuous so breeding birds are more easily noticed by predators and more likely to be targeted by humans, either for management or to harvest the birds’ guano for fertilizer (Danchin and Wagner 1997; Szpak et al. 2012).

One of the most important aspects of colonies is that they contain many different individuals living in close proximity. This type of aggregation can have both positive and negative effects since it facilitates the finding of mates and may help in giving information about food locations, but it can also promote competition and aggressive interactions (Burger 1983; Ellis and Good 2006; Somers et al. 2007). Competition for food and habitat are important in determining the reproductive success and survival of individuals (Schjørring et al. 1999; Forero et al. 2002). Colonial birds also compete for the best nesting locations, such as those in the centre or those obscured from predators (Schjørring et al. 1999). In order to determine which habitat is the best, some species prospect for ideal breeding territory by observing the number of young other individuals produced in other areas (e.g. Schjørring et al. 1999). Colonial birds compete for food either directly by piracy (García et al. 2014), or indirectly by exhausting the food within a given radius of the colony (Ashmole's Halo Hypothesis) (Ashmole 1963, e.g. Forero et al. 2002).

Aside from competition for habitat or food, birds in colonies frequently take part in aggressive interactions. Aggression is important as a way to defend young and preserve territorial boundaries (Hunt and Hunt 1976; Pius and Leberg 1997). Although physical injuries are rare when conspecifics engage in aggressive interactions, aggressive behaviours are still quite energetically costly (Neat et al. 1998). Some species such as ring-billed gulls (*Larus delawarensis*) may cannibalize other individuals' chicks, (Brown and Lang 1996) and other species including roseate terns (*Sterna dougallii)* kill unfamiliar young to ensure that they do not feed the wrong offspring accidentally (Ramos 2003). In mixed-species colonies, aggression is generally less intense because conspecifics interact more aggressively than with heterospecifics (Tinbergen 1953; Ellis and Good 2006; Somers et al. 2011). However, when two species of different sizes nest together, the larger one has less of a reason to fear injury, so it may outcompete the smaller one (see Gorski and Pajkert 1997). On the other hand, for some birds, nesting near another species may be beneficial, since aggressive interactions will be reduced compared to nesting near conspecifics (Ellis and Good 2006). Regardless of whether they nest in a single or mixed-species colony, colonial birds may usurp others' nests, harm young or otherwise act in a way that lowers other individuals' reproductive success or survival (Brown and Lang 1996; Skagen et al. 2001; García et al. 2014). Competition and aggression therefore play important roles in defining all aspects of a colony, including structure, breeding success and species composition.

The double-crested cormorant: overview of its uniqueness and history of management

Although 98% of all waterbirds nest in colonies, the double-crested cormorant (*Phalacrocorax auritus*) is somewhat unique in North America due to its life history and the context surrounding its impact and management (Rolland et al. 1998). Cormorants are highly adaptable and can nest in many environments successfully, including in trees or on the ground (Cuthbert et al. 2002; Somers et al. 2007). Their colony sizes can range from a few individuals to thousands (Wires and Cuthbert 2009). Cormorants are also somewhat unusual because they are able to transform their environment due to their acidic guano (Hebert et al. 2005). This excrement alters the pH and nutrient balance of the soil and kills trees (Hebert et al. 2005). Other species of waterbirds can impact vegetation with their guano, but cormorants have a larger, faster effect due to their high nest densities (Craig et al. 2012). Although cormorants alter ecosystems, this does not reduce the habitat they have available to them since tree-nesting cormorants can switch to nesting on the ground (Cuthbert et al. 2002; Somers et al. 2007). Cormorants are also interesting due to their relationship with other species of colonial waterbirds. Cormorants are attracted to areas that contain other colonial-nesting waterbirds and settle more frequently in new areas when other waterbirds are already present (Wires and Cuthbert 2009). Despite this, cormorants are frequently perceived to have a negative effect on other species because they alter the environment or usurp their nests (Gorski and Pajkert 1997; Jarvie et al. 1997; Skagen et al. 2001; Cuthbert et al. 2002; Somers et al. 2007). Although cormorants often interact aggressively with conspecifics, there are few records, to my knowledge, of direct aggression towards other species that affects their survival or breeding success (Somers et al. 2007). The interactions cormorants have with other species, their adaptability and their effect on habitat makes them valuable to study from a life-history perspective.

The uniqueness of double-crested cormorants in North America can make them a fascinating study species, but their reputation as a pest species (Hebert et al. 2005; Dorr et al. 2010; Dorr et al. 2014b) makes them an important species to study from a management perspective as well (Weseloh and Collier 1995; Wires and Cuthbert 2009). While cormorants have a negative reputation because they are perceived to cause the population decline or extirpation of other waterbirds, it is primarily their effect on fisheries and their ability to transform habitat that contributes to their image (Birt et al. 1987; Skagen et al. 2001; Cuthbert et al. 2002; Hebert et al. 2005; Somers et al. 2007; Dorr et al. 2010). Cormorant population was depressed from the 1950s to 1970s, due to excessive culling and widespread DDT use (Weseloh and Collier 1995). Once DDT was banned, cormorants rebounded and their population soared to never-before-seen levels due in part to the abundance of many high-quality small fish in lakes (Weseloh et al. 1995; Weseloh and Collier 1995). The population increase means that people are exposed more to cormorants than in recent memory, so the impact of their presence is larger and more noticeable.

Due to the perceived or real impact that cormorants have on habitat and fisheries, they are culled at a high rate (Weseloh and Collier 1995). Culling can be done through egg oiling or shooting, but often both methods are used (Dorr et al. 2010; Dorr and Somers 2012). Lethal control is so common that in 2007, some sort of management occurred at 64% of cormorant colonies on the US Great Lakes (Wires and Cuthbert 2009). The control of cormorants is not without controversy because cormorants do not impact fish or transform habitat everywhere where they are present, and their impacts are often exaggerated (Weseloh and Collier 1995; Wires 2015). Ground-nesting cormorants have less of an impact, since they nest in areas that are already barren and so cannot further transform habitat (Hebert et al. 2005). Cormorants can be culled as a preventative measure, or even if they have not had an impact at a site, so in many cases, culling may be overused as a management tool (Wires 2015).

Double-crested cormorants have extremely high population levels, although they are declining slightly in the Great Lakes, so their impacts on industry, habitat and on other species and their unique life history cannot be ignored (Weseloh and Collier 1995; Guillaumet et al. 2014; Dorr et al. 2014a). Their high population levels mean that density-dependent controls may be acting on the population, although the mechanism for this is unknown. From a management perspective, this is an important time to study cormorants in order to prevent their impact from increasing and the high cormorant population makes it easier than ever to study what makes them so unique from a life-history perspective in North America. Developing a broader understanding of this species both in single and mixed-species colonies can help create more effective and less invasive management techniques, help explain why cormorants are so successful and help in understanding cormorants' qualities. In Europe, the great cormorant, (*Phalacorcorax carbo*), has undergone similar population changes and has a similar life history and similar management issues as the double-crested cormorant, (see summary in Hatch et al. 2000) so this research can also help to understand more about other cormorant species.

In this thesis, I examine cormorants nesting on the ground and in the trees in both single and mixed-species colonies in Tommy Thompson Park in Toronto, Ontario. In particular, I explore the costs and benefits of competition and aggression for waterbirds in different colonies of double-crested cormorants. In the mixed-species colony, I examine if cormorants are responsible for a decline in black-crowned night herons (*Nycticorax nycticorax*) by examining indirect effects and direct aggression. In the single-species colony, I examine the impact that nest position and colony density had on aggression in double-crested cormorants and, if there is an effect, I further examine if aggression is related to parental behaviours or fledging success.

The effect of double-crested cormorants on the distribution and behaviour of breeding colonies of black-crowned night herons

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Abstract

Double-crested cormorants (*Phalacrocorax auritus*) nest in mixed-species colonies and are thought to extirpate other waterbirds, but it is unclear under what conditions this occurs and whether it is caused by direct or indirect effects. I examined if cormorants caused a decline in black-crowned night herons (*Nycticorax nycticorax*) at Tommy Thompson Park from 1992 to 2011, by analyzing nest positions and inter-specific interactions. I predicted that if cormorants negatively affected herons, heron population size, nest density and area occupied would decrease as cormorant density increased. Evidence for a negative indirect effect was only seen on Peninsula C of Tommy Thompson Park, where cormorants closely clustered near herons and their presence corresponded with reduced heron nest density and area occupied. Few direct aggressive inter-species interactions were observed, so more research is needed to determine how cormorants apparently cause heron decline. These long-term data indicate that cormorants can negatively impact other waterbird species.

Introduction

Coloniality is a breeding strategy found in almost all seabirds (Rolland et al. 1998). Although the exact reasons for colony formation are unknown for many species, birds may nest in these aggregations to protect themselves from predators, find food, or as a proximal way to find a high quality habitat or a mate (Birkhead 1977; Ward and Zahavi 1973; Zicus and Hennes 1989; Hoi and Hoi-Letner 1997). Many waterbirds nest in aggregations of two or more different species, known as mixed-species colonies, and can take advantage of the presence of another species for additional warnings about predator presence, or to acquire food (Nuechterlein 1981; Burger et al. 1983; Wojczulanis et al. 2004). However, mixed-species colonies may be beneficial for one species at the expense of another due to factors such as predation, parasite transmission or competition for food or for nesting space, which may cause one species to abandon the area (Jarvie et al. 1997; Gorski and Pajkert 1997; Valera et al. 2003; Ellis and Good 2006; Somers et al. 2007).

Double-crested cormorants (*Phalacrocorax auritus*) frequently nest in mixed-species colonies (Wires and Cuthbert 2009). This bird is considered a pest species in part because it is perceived to cause the population decline or extirpation of other native species of waterbirds that it nests with (Weseloh and Collier 1995). Both indirect and direct mechanisms have been proposed to explain how cormorants cause this decline. First, cormorants may alter the local habitat, thereby indirectly changing species composition and diversity and reducing nesting area (Hebert et al. 2005; Strickland et al. 2011). Secondly, cormorants may directly affect other waterbird species by aggressively interacting with them, such as by usurping their nests, or by fighting and outcompeting them for nesting space (Gorski and Pajkert 1997; Jarvie et al. 1997; Skagen et al. 2001; Cuthbert et al. 2002; Somers et al. 2007).

Tree-nesting cormorants can affect waterbirds in mixed-species colonies indirectly at both local and regional scales (Hebert et al. 2005). At the local scale, cormorants nest at very high densities compared to other waterbird species, so their nests can cause tree branches to break (Weseloh and Collier 1995; Craig et al. 2012). They also have highly acidic guano, which alters the soil pH and nutrient balance, leading to extensive tree mortality (Cuthbert et al. 2002; Hebert et al. 2005; Hebert et al. 2014). This changes the plant composition to include more non-native species and alters the arthropod community to include more dung-eaters (Strickland et al. 2011; Craig et al. 2012). In mixed-species colonies, these alterations can reduce tree-nesting habitat for other waterbirds. Birds nesting below cormorants will sometimes also abandon their nests because of the guano falling on them (Weseloh et al. 2002). At the regional scale, however, these changes may increase overall biodiversity due to increased habitat heterogeneity, but more work is required to fully understand these dynamics (Kolb et al. 2012).

It is unclear whether cormorants directly outcompete or interfere with other nesting waterbird species, thereby potentially leading to their decline (Cuthbert et al. 2002, Somers et al. 2007; Somers et al. 2011). Ground nesting double-crested cormorants nesting near herring gulls (*Larus argentatus*) in Saskatchewan appeared to dump eggs into their nests, while the herring gull population in Hamilton Harbour, Ontario, experienced lower nest success and declined due to interactions with cormorants (Somers et al. 2007; Somers et al. 2011). Great blue herons (*Ardea herodias*) that nested near cormorants experienced more interactions than when nesting near conspecifics, but the effect on fledging success was not measured (Wyman and Cuthbert 2015). In other locations, cormorants were able to coexist with other waterbird species including great blue herons, black-crowned night herons (*Nycticorax nycticorax*) and American white pelicans (*Pelecanus erythrorhynchos*) without affecting them due to either partitioning of nest area or due to cormorants' smaller size compared to other waterbirds, respectively (Cuthbert et al. 2002; Somers et al. 2011).

The black-crowned night heron frequently nests with cormorants and has the potential to be affected by them directly or indirectly due to its smaller size and use of trees as nesting sites (Wires and Cuthbert 2009; Hothem et al. 2010; Dorr et al. 2014). However, studies of the effect of cormorants on black-crowned night herons have been varied and contradictory. Cormorants have caused a decline in herons at Little Galloo Island in New York and, at other sites in the Great Lakes, cormorant guano rain has caused herons to abandon colonies (Cuthbert et al. 2002; Weseloh et al. 2002). At a site in Colorado, heron nests were usurped by cormorants and cormorants caused site abandonment (Skagen et al. 2001). Other studies, however, have found no relationship between cormorant presence and heron decline. Declines in herons at seven sites containing both species were attributed to a combination of normal vegetation succession not caused by cormorants, storms and human impacts rather than direct or indirect effects of cormorants (Cuthbert et al. 2002). Herons declined on West Sister Island, in Ohio, after cormorants arrived, but this equally could have been due to succession or cormorants (Shieldcastle and Martin 1997).

Cormorant colonies in Canada and the United States are often managed by culling or egg oiling (see Weseloh and Collier 1995; Johnson et al. 2015) due to their impact on fisheries or on habitat and vegetation (Dorr et al. 2010). The protection of species nesting in mixed-species colonies with cormorants is also cited as one of the reasons cormorants should be culled (Glahn et al. 2000; Strickland et al. 2011). These controversial management practices are not always completely justified or are overused, since cormorants can have neutral, rather than negative effects in some areas (Cuthbert et al. 2002; Wires 2015).

In this study, I explore the relationship between tree-nesting double-crested cormorants and black-crowned night herons at two peninsulas at Tommy Thompson Park (TTP), Ontario. Previous work done at this site (1992-1997) found that cormorants negatively affected herons by defoliating their nesting trees and by causing a shift in nesting locations (Jarvie et al. 1997). Cormorants also colonized herons’ new nesting areas after herons moved and the heron population declined as the cormorant population increased (Jarvie et al. 1997). I use a combination of longer-term spatial analyses of nest locations changes and recent behavioural observations of direct interactions between the species to test if cormorants are responsible for the decline in herons on TTP.

The hypothesis is that cormorants are affecting herons both directly and indirectly on both peninsulas due to a combination of the above-stated effects. I predict that if cormorants increase their population, nest density and sub-colony area over time, then this will correspond with a decrease in heron population, nest density and sub-colony area. Increased cormorant presence is also predicted to relate to a movement of herons away from areas of the highest cormorant concentration. If these negative effects directly affect herons, I expect to observe frequent aggressive inter-specific interactions and for cormorants to usurp higher numbers of nests as their population increases. If cormorants affect herons indirectly, such as by causing stress, defecating in their nests, or damaging trees, I predict their nests will be clustered close to herons, and the percent of trees co-occupied by herons and cormorants will increase with cormorant density.

Methods

Study Site

The Tommy Thompson Park (TTP) is located on a peninsula in Lake Ontario in Toronto, Canada (43_380N, 79_200W). TTP was designated as an Important Bird Area in 2000 by Birdlife International, and more than 296 species of birds have been observed there (Jarvie et al. 1997; Wilson and Cheskey. 2001). Seven species of colonial nesting waterbirds breed at the park and their nesting areas are protected and off-limits to the public during the breeding season. Some colonial nesting species (ring-billed gull, *L. delawarensis* and great egret *A. alba*) have been managed by encouraging or discouraging them from nesting in certain areas where competition or predation may be an issue (TRCA 2009). Since 2008, cormorants have been encouraged, through deterring tree-nesters and placing nest material on the ground, to nest on the ground, in order to preserve the trees (TRCA 2009; Wires and Cuthbert 2009).

Black-crowned night herons and double-crested cormorants have nested primarily on three sub-peninsulas jutting out of the western side of the main peninsula: Peninsulas A, B and C (Fig 1; summarized in Table 1). Herons first started nesting at TTP in 1979 on Peninsulas A and C, but, as of 2014, only nest on Peninsula B (181 nests) and Peninsula C (216 nests) (Fraser 1983 in Jarvie et al. 1997). Cormorants arrived at TTP on Peninsula B in 1990 and expanded to Peninsula C in 1998 (Jarvie et al. 1997; TRCA 2009). As of 2014, the majority of cormorant nests were on peninsulas B (7799 ground nests, 1319 tree nests) and C (3346 tree nests). (TRCA unpublished data). As of 2015, the cormorant colony at TTP is the largest in eastern North America (Wires 2015).

Temporal and spatial changes in nest patterns

GPS data on heron and cormorant nest positions were collected from 1992 to 2011 by the Toronto and Region Conservation Authority (TRCA) using a standardized protocol (see Jarvie et al. 1997). During the breeding season, each tree that contained a nest was mapped and trees that contained more than one nest were counted multiple times, giving metrics on nest density and movement over time. The relationship between heron and tree-nesting cormorant nest numbers overall and on all three peninsulas was calculated using Kendall's Tau correlation analysis, since the data were not normally distributed (Kendall 1938).

Spatial analyses, using ArcGIS 10.1 and R 3.1.3 (ESRI 2012; R Core Team 2015), were done only for peninsulas B and C because of the negligible number of birds of either species on Peninsula A. Nest density was calculated for each species each year using the Point Density tool with a cell size of 3 m and an optimal radius of 40 m estimated using Moran's I (ESRI 2012). Using these data, I determined the mean nest density for each species on each peninsula, the area occupied by each sub-colony, and the sub-colony's movements over time (ESRI 2012). To determine the percent of cormorants and herons that nested in the same tree each year, I used the Join tool to link together tree tags created for each nest by the TRCA (ESRI 2012). To find if cormorant nests indirectly affected herons through their presence at larger or smaller scales, I used the multitype L cross function, a transformation of the multitype K cross function, with 95% confidence intervals simulated after 999 iterations for scales ranging from 0-100 m with the spatstat 1.41-1 package (Dixon 2002; Baddeley and Turner 2005). This function calculates if cormorants were significantly clustered close to heron nests at different scales or significantly regularly distributed. The multitype K cross function is denoted as $K_{ij}(t) = \pi t^2$

where $K_{ij}(t)$ is the number of nests of j (cormorants) within a distance of t from all nests of i (herons). This is transformed to the multitype L cross function ($L_{ij}(t) = \left[\frac{K_{ij}(t)}{\pi}\right]^{0.5}$) due to its relatively constant variance. The function is corrected with Ripley's Isotropic Correction in order to correct for bias that may occur when measuring clustering in edge nests. The 95% confidence interval borders a theoretical stationary Poisson function, which is the ideal estimation for the multitype L cross function (Dixon 2002; Baddeley and Turner 2005).

Behavioural observations

Observations of direct interactions between herons and cormorants were made from 2013 to 2014 during the heron breeding season from May to July in order to quantify the frequency and severity of aggression between the two species. Observations were done one to three times a week on peninsulas B and C or in an area between the two peninsulas. Focal observations were accomplished by observing multiple independent randomly-chosen heron nests at once for 0.5 hr long periods from at least 15 m away from the nest. In 2013, 1 to 3 nests were observed simultaneously, while in 2014, three nests were observed together. The duration and type of each interaction (e.g., chases, physical contact, aggressive displays (e.g., heron forward threat; Hothem et al. 2010; cormorant threat call, stretching neck; Hatch et al. 1999), nest usurpation) was recorded to see if direct interactions occurred often enough to be an important mechanism for a heron decline.

Cormorant usurpation of heron nests was recorded from 2007-2014 on Peninsula C and in 2008, 2009, 2011 and 2014 on Peninsula B by following focal heron nests every week (Fraser unpublished data). Heron nests were mapped and checked weekly, and it was recorded whether they were occupied by a heron or a cormorant. The number of usurpations were quantified to determine if the majority of heron nests were affected and to give a possible mechanism for the heron decline. A Kendall's Tau correlation analysis was done to determine if the number of nest usurpations changed as the population of cormorants changed. The difference between nest usurpation rates on each peninsula each year was calculated using a Fisher's exact test (Fisher 1922; R Core Team 2015).

Results

Temporal changes in population size

The relationship between the populations of cormorants and herons differed between the two peninsulas. Overall, there was not a significant relationship between the number of heron and cormorant nests over time at TTP (tau b=0.037 p=0.88) (Fig 2d). On Peninsula A, heron numbers remained low over time, while cormorant numbers increased greatly from 1992 (12 nests, Fig 2a), to 2000 (933 nests) before declining to another low (19 nests) in 2011. On Peninsula B, there was no relationship between the number of heron and cormorant nests (tau b=0.22, p=0.18) (Fig 2b). Both species' population levels peaked in the early 2000s and then declined until 2011, but prior to 2002, the population changes between species were not similar. On Peninsula C, there was a significant negative relationship (tau b=-0.49 p=0.041) between the number of heron and cormorant nests present from 2001 onwards, after cormorants colonized the peninsula. Heron nests increased sharply from 1993 to 1996, (0 to 1086 nests) then remained relatively stable until 2003 and began to decline soon after cormorants arrived (Fig 2c).

Spatial patterns over time

I predicted that an increase in cormorant nest density and sub-colony area over time would correspond to a decrease heron nest density and sub-colony area and that cormorant presence would be related to a movement of herons away from cormorant nesting areas. These predictions were tested on separate sub-colonies at Peninsula B and Peninsula C. On Peninsula B, cormorants and herons occupied overlapping areas most years (Fig 4, Fig 5). Herons tended to move to new areas first, with cormorants following in the next few years. Both species had low densities in 1992 (heron mean density 0.16 nests/100 m^2, SD 0.074, cormorant mean density 0.32 nests/100 m^2 SD 0.23). From 1992 to 2001, cormorant density and area occupied increased as heron density and area occupied slightly decreased, although an increase in heron density in 2000 (0.73 nests/100 m^2 SD= 0.93) confounded that trend. From 2004 to 2011, both species' nest densities and occupied areas decreased (Fig 3a).

On Peninsula C, herons first arrived in 1994 (mean density 0.86 nests/100 m^2, SD 1.1) and nested in the middle of the peninsula, while cormorants only started nesting on the peninsula in large numbers in 2001. Cormorants settled in the same area that herons were already occupying (Fig 6, Fig 7). Cormorants and herons nested in the same area until 2004, during which time cormorant nest density increased substantially and the area they occupied more than doubled compared to 2000 (43665 m^2). After 2004, herons began to move more inland towards the areas where cormorants had a lower density, although a portion of their nests always overlapped. Heron area occupied declined from 2004 to 2011, while the area occupied by cormorants increased and then stabilized over the same period. Cormorant nest density increased from 2000 to 2007 and then stabilized before declining in 2009, and heron nest density declined from 2000 to 2011 (Fig 3b).

I predicted that cormorants could indirectly affect herons by clustering near them, since this could affect them by causing stress, defecating in their nests, or damaging trees. On Peninsula B, cormorant nests were significantly clustered near heron nests in some years, but not others (Fig 8). On both peninsulas, cormorants tended to significantly cluster near heron nests when considering the nests at broader scales (20-100m). However, when observing them at smaller scales (0-20m), cormorant nests were regularly distributed most years. On Peninsula C, cormorants were significantly clustered near heron nests at most scales in almost twice as many years as on Peninsula B (12 years vs 7 years) (Fig 8). On Peninsula C, clustering occurred at least once at some scale in 9 of 16 years where both species were present, while on Peninsula B, clustering was observed for 12 of 18 years when both species were present. Overall, cormorants were more often clustered close to herons on Peninsula C than Peninsula B.

I predicted that cormorants could affect herons indirectly by nesting on the same tree since they could defecate in heron nests or cause stress by nesting so close. Cormorants and herons rarely nested on the same tree on Peninsula B but did so more often on Peninsula C (Fig 9a). Of the 18 years that both species were present on Peninsula B, there were only 4 years in which cormorants occupied more than 10% of trees that herons nested on. On Peninsula C, cormorants rarely occupied the same tree as herons from 1992 to 2000 since cormorants were rarely present at that time. Beginning in 2000, the percent of co-occupied trees increased, peaking in 2010 at 43%. The percent of heron trees occupied by cormorants was significantly positively correlated with mean cormorant density (tau b=0.71 p=0.045) on Peninsula C, but not on Peninsula B (tau b=-0.23 p=0.21) (Fig 9b).

Behavioural observations

I predicted that cormorants could affect herons directly by usurping their nests more often as cormorant population increased, or by interacting with them. Out of 368 nest observations (68 in 2013, 300 in 2014 for a total of 61.5 hours), I only observed two direct interactions between herons and cormorants each year. When observing nest usurpations, 1035 heron nests were followed from 2007 to 2014 but on average, only 5.0% of nests were usurped each year. Although the population of cormorants increased on Peninsula C and decreased on Peninsula B during this time, there was no relationship between the percent of nest usurpations and the number of cormorants on Peninsulas B and C each year, (Peninsula B tau b=-0.33, p=1, Peninsula C tau b=0.40, p=0.48) nor did the number of nest usurpations vary between peninsulas (2008 p=1, 2009 p=0.18, 2011 p=0.26, 2014 p=0.59).

Discussion

I examined if double-crested cormorants were responsible for the decline in black-crowned night herons observed at TTP and if they caused a decline through indirect or direct mechanisms. Cormorants seemed to have a negative effect on herons on both peninsulas, but the largest potential effect was observed on Peninsula C, where heron nest density, sub-colony area and population size declined as these factors increased for cormorants. Herons also moved away from areas of highest cormorant concentration. On Peninsula B, the cormorant population was not correlated with the heron population, cormorants and herons occupied overlapping areas and cormorants displayed similar patterns in nest density and area occupied to herons in more than half the years they were observed. On both peninsulas, direct interactions rarely occurred and nest usurpations were infrequent and unrelated to cormorant population size. Indirect effects, such as a correlation between co-occupied trees and cormorant population, were only observed on Peninsula C. Cormorants also clustered closer to herons more frequently and at more scales on Peninsula C than Peninsula B. These results show that cormorants seemed to play a role in the decline of herons at TTP, through indirect, not direct effects and that they had a much stronger and more noticeable impact on Peninsula C. Although there were a few isolated instances where cormorants seemed to affect herons on Peninsula B, the sum of all the data point to the conclusion that their effect was negligible. These results only partially support the hypothesis: that cormorants cause declines through indirect and direct effects on both peninsulas, because this seemed to occur only on Peninsula C where cormorant density and population size were very high, and cormorants appeared to be affecting herons indirectly. Notably, these results contradict the conclusion reached by Jarvie et al. (1997) at this site: that cormorants caused a decline in herons on Peninsula B from 1992, primarily because of the heron resurgence and increase in nest density that occurred in the 2000s.

Cormorants seemed to have affected herons more on Peninsula C compared to Peninsula B, and this may be for several reasons. Due to the high cormorant density, high overall population levels and high percent heron tree occupancy on Peninsula C, herons were consistently exposed to more cormorants, which could have increased their stress levels or altered their behaviour. Higher nest densities around breeding king penguins (*Aptenodytes patagonicus*) in a colony was correlated with an increase in stress levels, so something similar may occur in herons (Viblanc et al. 2014). There may be a threshold at which the density and population of cormorants in an area is too high, above which herons become too stressed and abandon the area. This would explain why cormorants affected herons more on Peninsula C, despite the two peninsulas having a similar number of cormorants some years. Since cormorants nested on the same trees as herons more on Peninsula C, this increased the chance that they defecated into heron nests, which has been shown to cause nest abandonment at other sites (Weseloh et al. 2002).

There was no evidence that cormorants and herons directly interacted with each other at heron nests. Only four interactions were observed over two years, cormorants were never seen usurping herons’ nests despite evidence that it occurred and nest usurpation rate did not change as cormorant population changed. Anecdotal evidence of interactions exists for TTP (Jarvie et al. 1997; GS Fraser pers. comm) and there have been interactions and nest usurpations observed between herons and cormorants at other sites (Skagen et al. 2001). The lack of interactions observed during the study periods may have been due to bias caused by the presence of the observer near focal nests, but this is unlikely since care was taken to avoid disturbances. Cormorants may also interact with herons for intense short bursts, such as pushing one bird off a nest to take it over, that would have a large impact, but be easy to miss using 30 min focal observations, so scanning for interactions may be a more effective approach for future research. Conversely, cormorants may not be forcing herons to abandon nests at all. Predation, disease or other factors may leave a heron nest empty, allowing an opportunistic cormorant to occupy it without directly interacting with a heron.

Cormorants seemed to affect herons indirectly since their presence corresponded with a shift in heron spatial distribution, and because cormorants clustered near herons, effectively reducing their nesting area. To my knowledge, this is the first time that cormorants have been associated with a decline in herons in this manner, since in other studies, cormorants affected herons directly by usurping their nests or by defecating in them, or there was no explanation for how they caused a decline (Skagen et al. 2001; Cuthbert et al. 2002; Weseloh et al. 2002). Other studies have proposed that cormorants would reduce nesting area for other waterbird species by killing trees, but at this site, herons nested on healthy trees and there was always forest available to them, which means that this was not likely to be a major factor in their decline (Hebert et al. 2005; TRCA unpublished data). Deterrent activities by the TRCA also prevented cormorants from expanding their nesting area into all the places where herons nest, so there was habitat available for both of these species (TRCA unpublished data). Other species of herons and cormorants can benefit from living in mixed-species colonies. Great cormorants (*P. carbo*) had a positive effect when they nested near grey herons (*A. cinerea*) since regurgitated food was an important food source for recently fledged grey heron young that were not yet adept at hunting on their own (Wojczulanis et al. 2004). Although the same behaviour has been observed at TTP, there is no evidence that this offsets the negative effect of cormorants on herons (GS Fraser pers. comm.).

Other factors, such as predation, likely play a role in the heron decline at TTP. Herons were declining on both Peninsulas B and C, despite cormorants only strongly associating with their decline on Peninsula C. As of 2002, the Great Lakes heron population is stable or increasing overall, so birds at TTP may have been abandoning the site and choosing to nest elsewhere (Cuthbert et al. 2002). Raccoon (*Procyon lotor*) predation may play more of a role in the decline of herons at TTP compared to other sites because herons usually nest on mammal-free islands (Fraser and Conliffe 2014). Invasive fire ants (*Myrmica rubra*) exist at much higher than normal densities at TTP, and they may kill young heron chicks (Ito and Fraser 2015, but see Rudmik 2011). Since colonial birds can measure the quality of a site based on the success of their neighbours, frequent nest failures due to predation may lead herons to choose other sites

(Schjørring et al. 1999; Hénaux et al. 2007). Factors that affect herons in other sites, such as vegetation succession and storms, are likely to have less of an impact at TTP, because herons nest high on trees, while in other sites they tend to nest in bushes or closer to the ground (Cuthbert et al. 2002; Hothem et al. 2010). Birds nesting in trees are also not at risk of loss of nesting substrate due to succession, since forests are more often in a climax form of succession compared to areas with bushes. Herons that nested in mixed-species colonies with cattle egrets (*Bubulcus ibis*) and little egrets (*Egretta garzetta*) at a site in the Caspian Sea were more successful when nesting higher in trees, further supporting the idea that herons are not abandoning TTP because their nesting area is not suitable (Ashoori and Barati 2013). Although many of the issues affecting other sites are not relevant at TTP, it is likely that a combination of factors affect herons at this site and future research should focus on how they all contribute to the heron decline.

Although nesting in a mixed-species colony was likely not beneficial for herons, this nesting arrangement is ongoing as of 2015. Cormorants may have been benefiting from nesting near herons and by initially following them into new nesting areas. At TTP, cormorants only moved to new areas of the peninsulas after herons were present. This may be because cormorants generally prefer and benefit from nesting in mixed-species colonies on the Great Lakes (Wires and Cuthbert 2009). They nest most often with great blue herons, black-crowned night herons, herring gulls or ring-billed gulls (Wires and Cuthbert 2009). At other colonies, only 3% of cormorants established themselves in new areas if other waterbirds were not present (Wires and Cuthbert 2009). Birds may form colonies in new areas based on the presence of other species, so cormorants may use heron presence as a marker of habitat quality when deciding whether to breed in new areas (Forbes and Kaiser 1994). This also provides an explanation why cormorants clustered close to herons, even when herons continuously moved away from where the bulk of the cormorant colony is situated. Cormorants nesting with great blue herons expended less energy and had fewer interactions than when nesting near conspecifics, so nesting near black-crowned night herons may benefit cormorants in the same way (Wyman and Cuthbert 2015). Birds can also benefit from nesting in mixed-species colonies due to increased predator protection or because they work together to find food (Burger 1983; Ward and Zahavi 1973). It is not likely that predator protection encourages cormorant clustering near herons because herons do not respond to predators in an obtrusive way by mobbing them (Forbes 1989). Cormorants and herons have different foraging strategies, so cormorants are not likely to rely on herons for food (Hothem 2010, Dorr et al. 2014).

Since cormorants seemed to be negatively affected herons, management may be useful to help to preserve the heron colony at TTP. Herons have been declining overall at this site, despite the efforts of the managers to restrict cormorants to certain areas. Although it is likely that cormorants were not the only factors contributing to the decrease in the heron population, a more aggressive management strategy may benefit herons, particularly on Peninsula C.

Literature Cited:

Ashoori A, Barati A. 2013. Breeding success of black-crowned night heron (*Nycticorax nycticorax*), little egret (*Egretta garzetta*) and cattle egret (*Bubulcus ibis*) (Aves: Ardeidae) in relation to nest height in the South Caspian Sea. Ital. J. Zool. 80(1): 149-154.

Baddeley A, Turner R. 2005. Spatstat: An R package for analyzing spatial point patterns. Journal of Statistical Software. 12(6):1-42. Available from: http://www.jstatsoft.org/v12/i06/

Birkhead TR. 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). J. Anim. Eco. 46(3): 751-764.

Burger J. 1983. Grebes nesting in gull colonies: protective associations and early warning. Am Nat. 123(3): 327-337.

Craig EC, Elbin SB, Danoff-Burg JA, Palmer MI. 2012. Impacts of double-crested cormorants (*Phalacrocorax auritus*) and other colonial waterbirds on plant and arthropod communities on islands in an urban estuary. Waterbirds. 35(SUPPL. 1):4-12.

Cuthbert FJ, Wires LR, McKearnan JE. 2002. Potential impacts of nesting double-crested cormorants on great blue herons and black-crowned night-herons in the U.S. Great Lakes region. J. Great Lakes Res. 28(2):145-154.

Dixon PM. 2002. Ripley’s K function. In: El-Shaarawi AH, Peigorsch WW, editors. Encyclopedia of Environmetrics Vol 3. Chichester. John Wiley & Sons. p1796-1803

Dorr BS, Aderman T. Butchko PH, Barras SC. 2010. Management effects on breeding and foraging numbers and movements of double-crested cormorants in the Les Cheneaux Islands, Lake Huron, Michigan. J. Great Lakes Res. 36(2): 224-231.

Dorr BS, Hatch JJ, Weseloh DVC. 2014. Double-crested Cormorant (*Phalacrocorax auritus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; [cited 2015 Jun 18] Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/441

Ellis JC. Good TP. 2006. Nest attributes, aggression, and breeding success of gulls in single and mixed species subcolonies. Condor. 108(1):211-219.

ESRI 2012. ArcMap 10.1 Build 3035. Redlands CA: Environmental Systems Research Institute.

Fisher RA. 1922. On the interpretation of $\chi 2$ from contingency tables, and the calculation of P. J R Stat Soc 85(1):87–94.

Forbes SL. 1989. Coloniality in herons: Lack’s predation hypothesis reconsidered. Colon. Waterbird. 12(1): 24-29.

Forbes SL, Kaiser GW. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. Oikos. 70(3): 377-384.

Fraser GS, Conliffe S. 2014. A report on work related to Black-crowned Night Herons on Peninsula C, Tommy Thomson Park, April-August 2014. TRCA. 9 p.

Glahn JF, Tobin ME, Blackwell BF. 2000. A science-based initiative to manage double-crested cormorant damage to southern aquaculture. USDA National Wildlife Research Center-Staff Publications. Paper 532. 38 p.

Gorski W and Pajkert Z. 1997. Interactions between cormorants *Phalacrocorax carbo* and herring gulls *Larus argentatus* in their common breeding sites. Pol. J. Ecol. 45(1): 161-164.

Hebert CE, Duffe J, Weseloh DVC, Senese TEM, Haffner DG. 2005. Unique islands habitats may be threatened by double-crested cormorants. J Wildlife Manage. 69(1):68-76.

Hebert CE, Pasher J, Weseloh DVC, Dobbie T, Dobbyn S, Moore D, Minelga V, Duffe J. 2014. Nesting cormorants and temporal changes in island habitat. J Wildlife Manage. 78(2):307-313.

Hénaux V, Bregnballe T, Lebreton J. 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. J. Avian Biol. 38(1):44-57.

Hoi H, Hoi-Leitner M. 1997. An alternative route to coloniality in the bearded tit: Females pursue extra-pair fertilizations. Behav. Ecol. 8(2):113-119.

Hothem RL, Brussee BE, Davis WE Jr. 2010. Black-crowned Night-Heron (*Nycticorax nycticorax*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; [Internet] [cited 2015 Jun 18]. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/074

Ito N, Fraser GS, Packer L. 2015. Abundance and distribution of European fire ant (*Myrmica rubra*) on 15 TRCA sites. A report submitted to the TRCA, April 2015. 24 pgs.

Jarvie S, Blokpoel H and Chipperfield D. 1997. A geographic information system to monitor nest distributions of double-crested cormorants and black-crowned night-herons at shared colony sites near Toronto, Canada. Symposium on Double-Crested Cormorants: Population Status and Management Issues in the Midwest. Paper 13. Available from: http://digitalcommmons.unl.edu/nwrccormorants/13

Johnson JH, McCullough RD, Farquhar JF, Mazzocchi I. 2015. Little Galloo Island, Lake Ontario: Two decades of studies on the diet, fish consumption and management of double-crested cormorants. J. Great Lakes Res. 41(2):652-658.

Kendall M. 1938. A New Measure of Rank Correlation. Biometrika. 30(1–2): 81–89.

Kolb GS, Jerling L, Essenberg C, Palmborg C, Hambäck PA. 2012. The impact of nesting cormorants on plant and arthropod diversity. Ecography. 35(8):726-740.

Nuechterlein GL. 1981. ‘Information parasitism’ in mixed colonies of western grebes and Forster’s terns. Anim Behav. 29(4): 985-989.

Pearson K. 1900. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. Philos. Mag. Ser. 5. 50(302): 157–175.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org/.

Rolland C, Danchin E, de Fraipont M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Am. Nat. 151(6):514–529.

Rudmik K. 2011. Invasive European fire ants (*Myrmica rubra*) in an urban green-space: abundance, distribution and impact on tree nesting black-crowned night herons [dissertation]. York University. 70 p.

Schjørring S, Gregersen J, Bregnballe T. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. Anim. Behav. 57(3): 647-654.

Shieldcastle MC and Martin L. 1997. Colonial waterbird nesting on West Sister Island National Wildlife Refuge and the arrival of double-crested cormorants. Paper presented at: Symposium on double-crested cormorants: population status and management issues in the Midwest. 12p.

Skagen SK, Melcher CP, Muths E. 2001. The interplay of habitat change, human disturbance and species interactions in a waterbird colony. Am. Midl. Nat. 145(1):18-28.

Somers CM, Doucette JL, Weseloh DVC, Kjoss VA and Brigham RM. 2011. Interactions between double-crested cormorants and other ground-nesting species. Waterbirds. 34(2): 168-176.

Somers CM, Lozer MN, Quinn JS. 2007. Interactions between double-crested cormorants and herring gulls at a shared breeding site. Waterbirds. 30(2):241-250.

Strickland BK, Dorr BS, Pogmore F, Nohrenberg G, Barras SC, McConnell JE, Gobeille J. 2011. Effects of management on double-crested cormorant nesting colony fidelity. J. Wildlife Manage. 75(5): 1012-1021.

[TRCA 2009] The Toronto and Region Conservation Authority Index to Authority Meeting #2/09. 2009. [Internet] [cited 2015 Apr 15] Available from: http://tommythompsonpark.ca/global/pdfs/AuthorityAgenda02-09-March27_2009.pdf

Valera F, Casas-Criville A, Hoi H. 2003. Interspecific parasite exchange in a mixed colony of birds. J. Parasitol. 89(2): 245-250.

Viblanc VA, Gineste B, Stier A, Robin J-, Groscolas R. 2014. Stress hormones in relation to breeding status and territory location in colonial king penguin: A role for social density? Oecologia. 175(3): 763-772.

Ward P, Zahavi A. 1973. The importance of certain assemblages of birds as “information-centres” for food finding. Ibis. 115(4): 517-534.

Weseloh DV, Collier B. 1995. The rise of the double-crested cormorant on the Great Lakes: Winning the war against contaminants. Environment Canada. 12 p.

Weseloh DVC, Pekarik C, Havelka T, Barrett G, Reid J. 2002. Population trends and colony locations of double-crested cormorants in the Canadian Great Lakes and immediately adjacent areas, 1990-2000: A manager’s guide. J. Great Lakes Res. 28(2): 125-144.

Wilson, W. G. and E. D. Cheskey 2001. Leslie Street Spit – Tommy Thompson Park Important Bird Area Conservation Plan. Can. Nature Fed., Bird Studies Can., Fed. of Ont. Naturalists. 56 pp

Wires LR, Cuthbert FJ. 2009. Characteristics of double-crested cormorant colonies in the U.S. Great Lakes island landscape. J. Great Lakes Res. 36(2):232-241.

Wires LR. 2015. Migratory bird protection, a crack in the armor: the case of the double-crested cormorant. Avian Conser. Ecol. 10(1). Available from: http://dx.doi.org/10.5751/ACE-00761-100108

Wojczulanis K, Takubas D, Stempniewicz. 2004. Exploitation by the grey heron of fish regurgitated by cormorants. Waterbirds. 28(2):225-229.

Wyman KE, Cuthbert FJ. 2015. Species identity and nest location predict agnostic interactions at a breeding colony of double-crested cormorants (*Phalacrocorax auritus*) and great blue herons (*Ardea herodias*). Waterbirds. 38(2): 201-207.

Zicus MC, Hennes SK.1989. Nest prospecting by common goldeneyes. Condor. 91(4): 807-812.

Tables

Table 1: Summary values for density and population of black-crowned night herons (BCNH) and double-crested cormorants (DCCO) on peninsulas B and C, Tommy Thompson Park, Toronto, Canada.

	Peninsula	**Year of arrival**	**Year of peak mean density**	**Year of peak population size (# of nests)**	**Peak mean density (nests/m^2)**	**Peak population size (# of nests)**
BCNH	**Pen B**	1992	2004	2004	0.0140	260
	Pen C	1994	1996	1996	0.0238	1086
DCCO	**Pen B**	1990	2001	2003	0.0398	2409
	Pen C	1993	2007	2007	0.0509	3977

Figures

Figure 1: Map of the Leslie Street Spit in Toronto, Ontario, showing the locations of Peninsulas A, B and C, which are inhabited by sub-colonies of birds. As of 2014, Peninsula A contains ground and tree-nesting double-crested cormorants, Peninsula B contains black-crowned night herons and ground and tree-nesting cormorants and Peninsula C contains tree-nesting cormorants and herons.

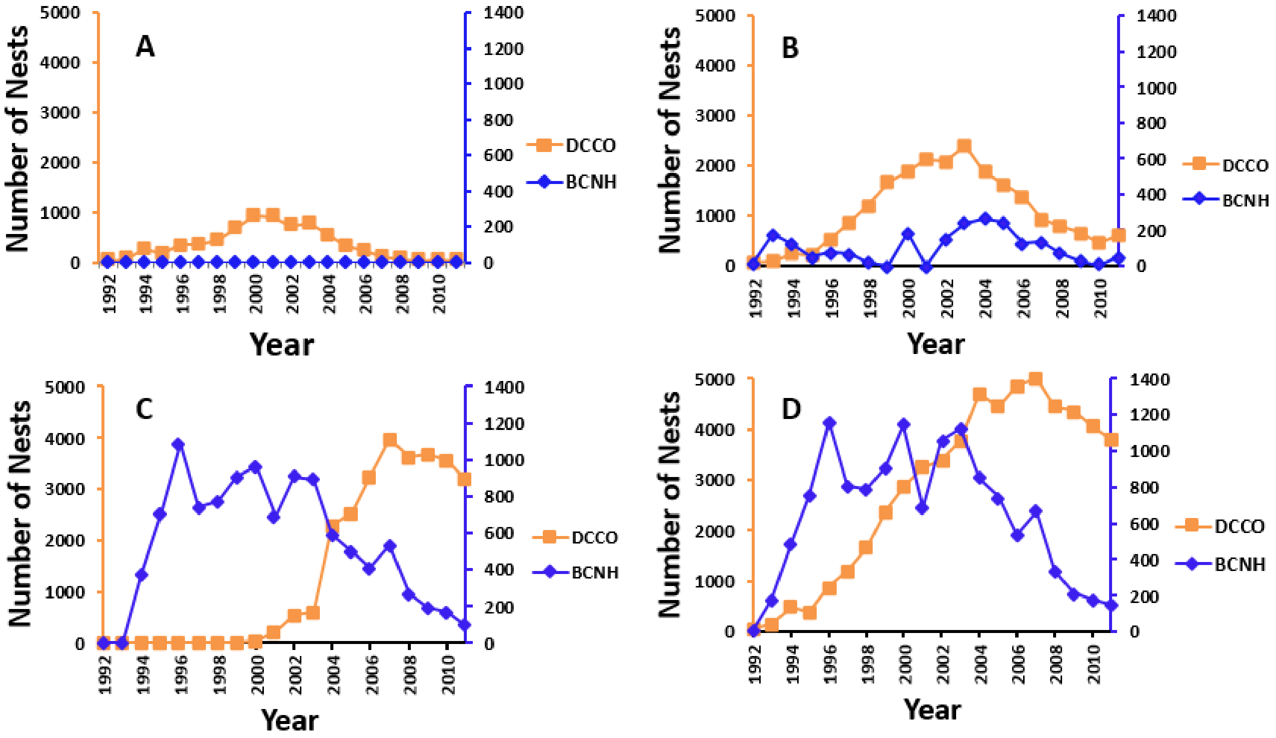


Figure 2: The number of black-crowned night heron (BCNH) nests compared to the number of tree-nesting double-crested cormorant (DCCO) nests from 1992 to 2011. Figure 2a) shows the number of birds on Peninsula A and figures 2b) and 2c) and 2d) show the numbers for Peninsulas B and C, and overall on all three peninsulas, respectively. All cormorant numbers are plotted on the primary axis and all heron numbers are plotted on the secondary axis.

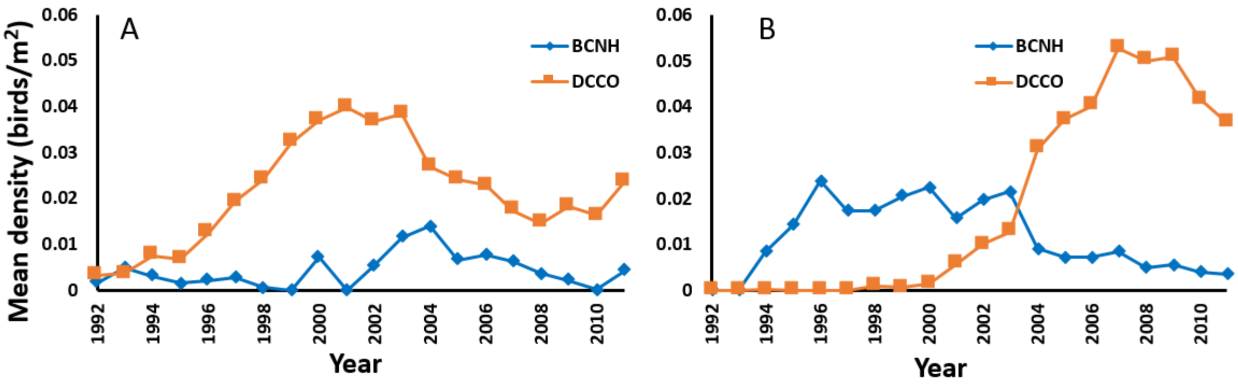
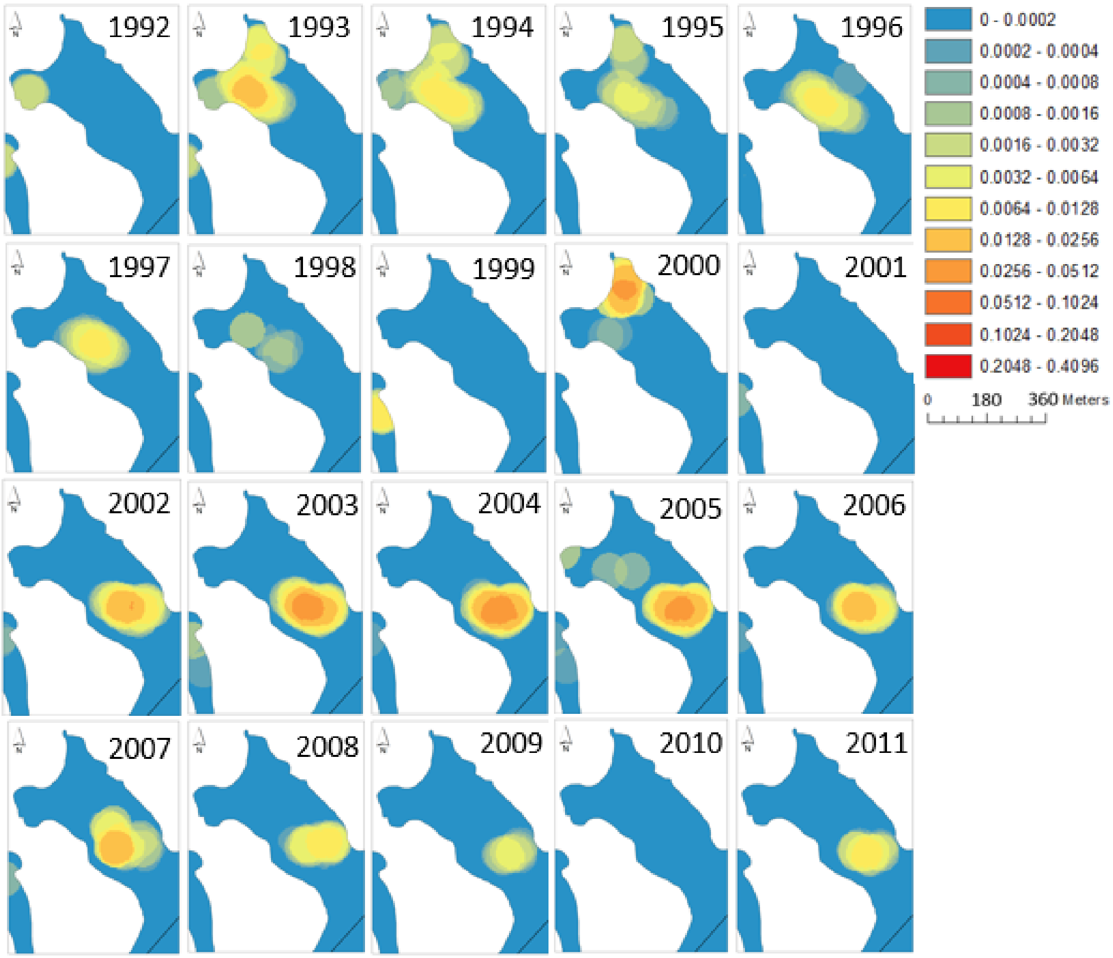


Figure 3: Mean density of black-crowned night heron (BCNH) and double-crested cormorant (DCCO) nests from 1992 to 2011. Figure 3a shows the density of nests on Peninsula B and figure 3b shows the density on Peninsula C.



<u>Figure 4:</u> Density (nests/m^2) and area (m^2) occupied by black-crowned night heron nests on Peninsula B of the Leslie Street Spit from 1992-2011.

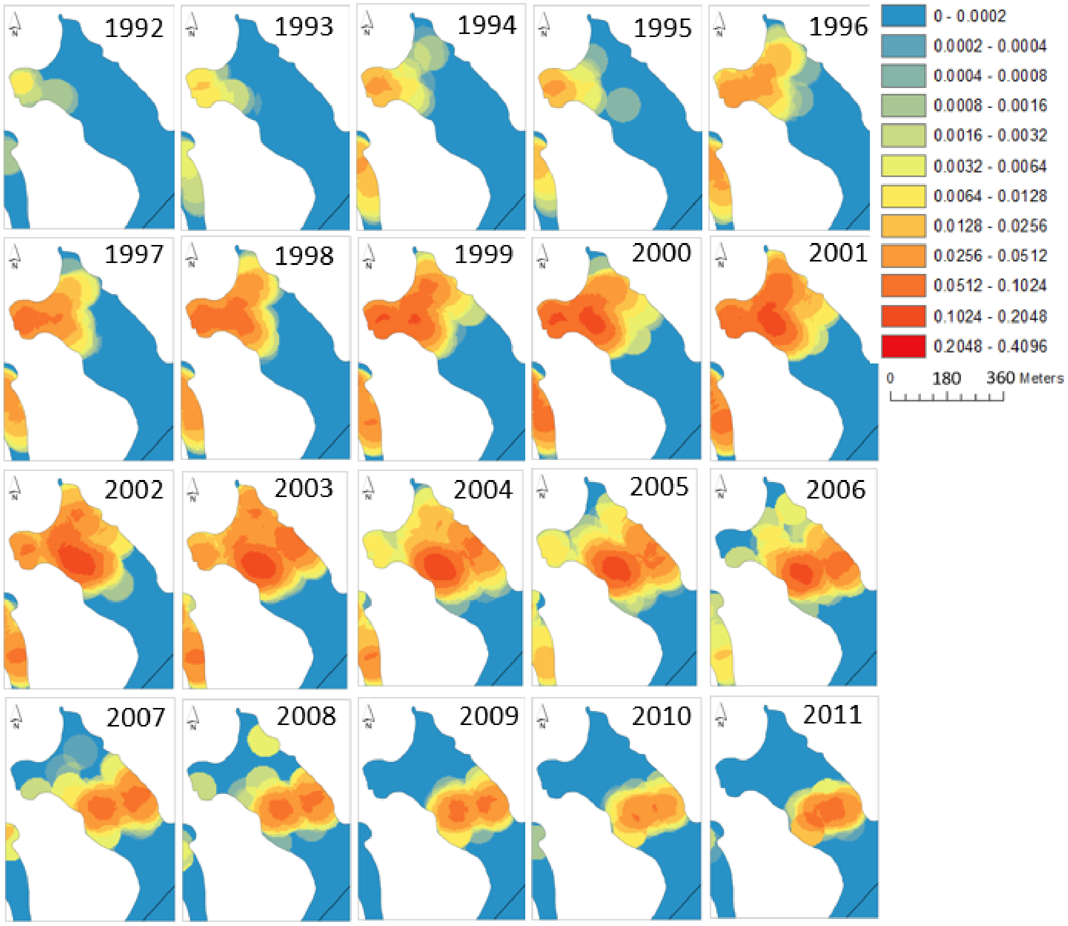


Figure 5: Density (nests/m^2) and area (m^2) occupied by double-crested cormorant nests on Peninsula B of the Leslie Street Spit from 1992-2011.

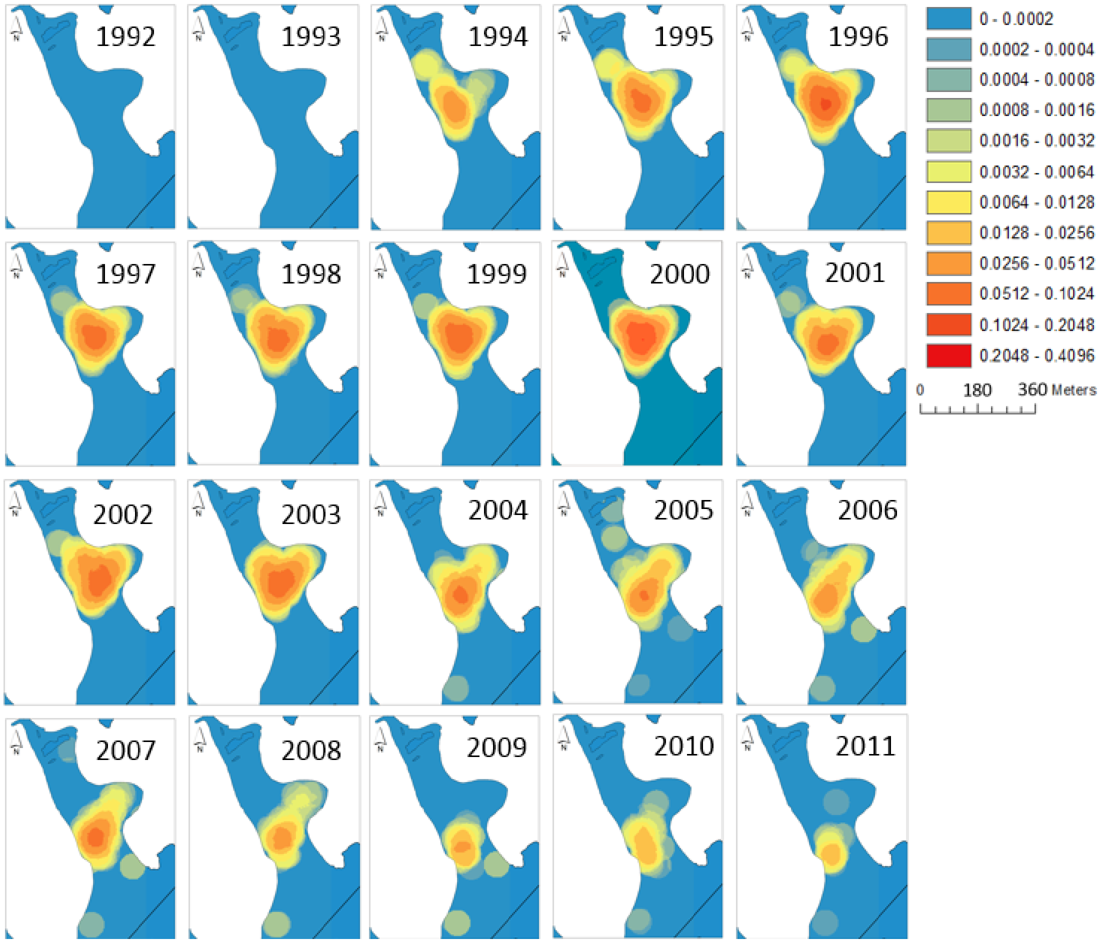


Figure 6: Density (nests/m^2) and area (m^2) occupied by black-crowned night heron nests on Peninsula C of the Leslie Street Spit from 1992-2011.

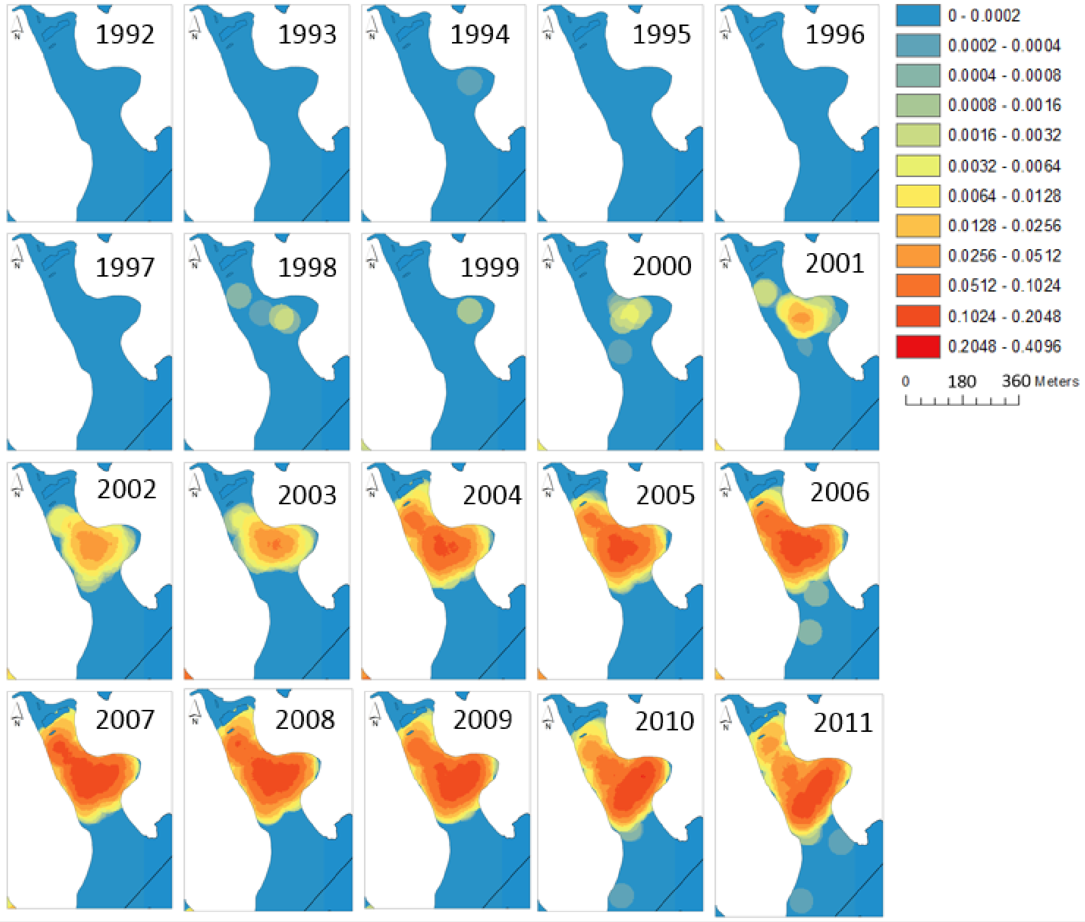


Figure 7: Density (nests/m^2) and area (m^2) occupied by double-crested cormorant nests on Peninsula C of the Leslie Street Spit from 1992-2011.

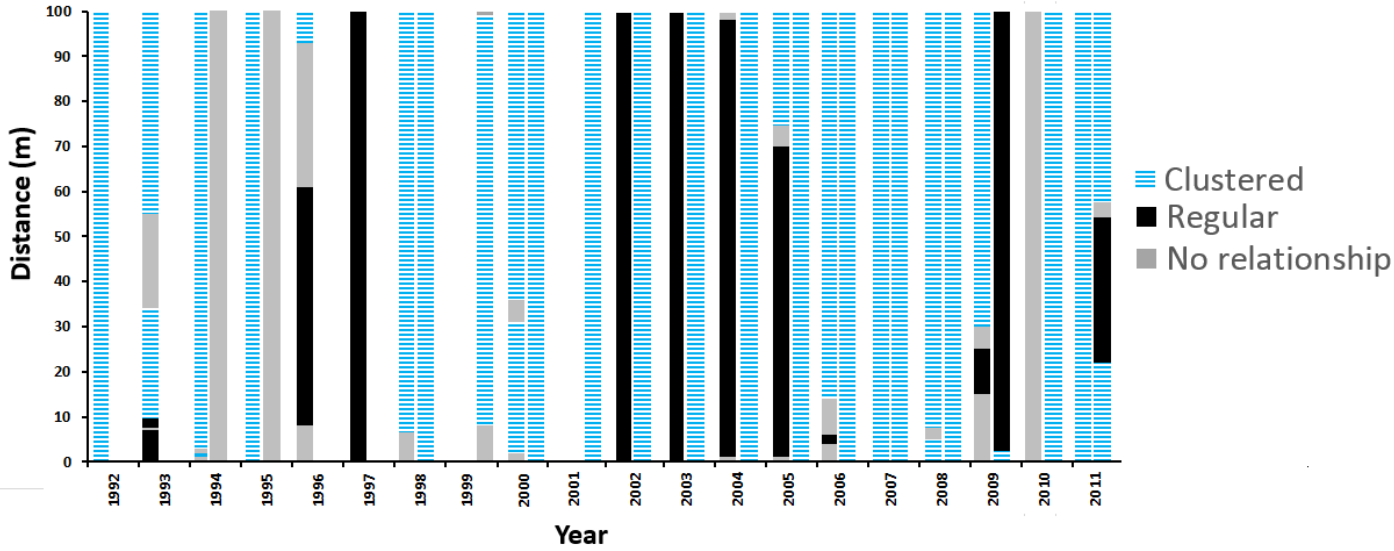


Figure 8: The distance scales at which double-crested cormorant nests are clustered or randomly distributed around black-crowned night heron nests on Peninsula B (left column) or Peninsula C (right column) from 1992 to 2011. Areas in stripes indicate that cormorant nests were significantly clustered close to heron nests when observing patterns at those scales, areas in black are where they are significantly regularly distributed and areas in grey indicate no significant relationship at those scales.

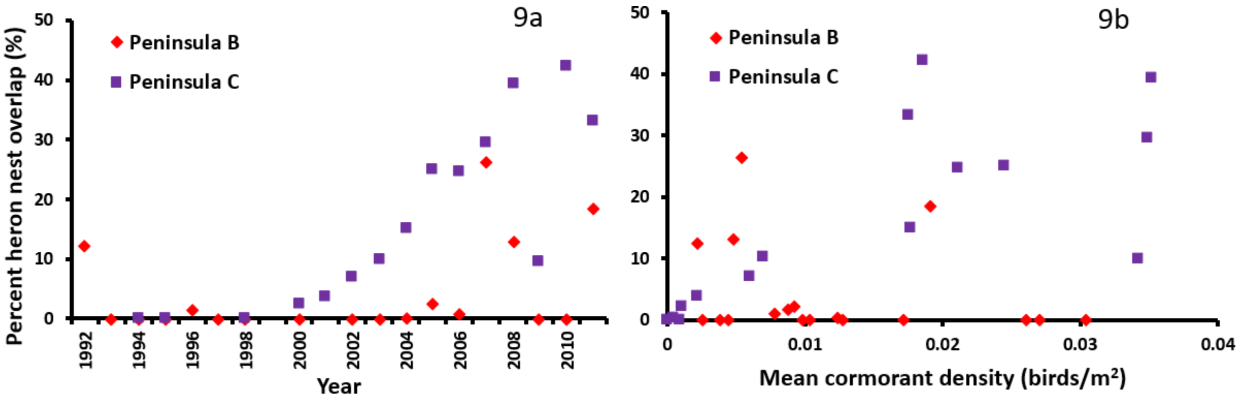


Figure 9: Percent of trees that contained black-crowned night heron nests that also contained double-crested cormorant nests on Peninsulas B and C from 1992 to 2011 (9a) and its relationship to mean cormorant density (9b). Only years where both species were present on a peninsula are shown.

Analysis of behaviour trade-offs and their relationship to density, position and fledging success in ground-nesting double-crested cormorants

Lisa Charlotte Rosenberger

Abstract

In colonies, spatial structure is important in influencing the behaviour of individuals due to variation in nest density and position. In turn, behaviour may influence reproductive success either directly or through trade-offs. I examine if the density and position of nests in a ground-nesting colony of double-crested cormorants (*Phalacrocorax auritus*) impacts aggressive behaviour. I further explore if aggression and parental behaviour affect fledging success, either directly or through a trade-off between the behaviours. Based on focal observations, aggression increased as density decreased in the colony, however, nest position had no significant effect on aggression. Parental behaviour was positively correlated with aggression so there was no evidence of a trade-off, and there was no relationship between parental or aggressive behaviour and fledging success. The results indicated that density-dependent effects on behaviour are not yet important in regulating cormorant population levels at this site.

Introduction

Breeding colonies are very common in birds, especially seabirds, having evolved independently at least 21 times (Rolland et al. 1998). Many factors affect the breeding success and survival of colonial birds, such as the presence of other species, colony size and breeding synchrony (Burger 1983; Clode 1993; Hernández-Matías et al. 2003; Ellis and Good 2006; Jovani and Grimm 2008). Two factors, the density of the colony and an individual's location in the colony, have been well studied and are important in affecting a bird's survival and fledging success (Danchin and Wagner 1997; Phillips 1998; Hötker 2000; Stokes and Boersma 2000; Ashoori and Barati 2013; Minias and Kaczmarek 2013; Liordos and Lauder 2015). Birds that nest in dense aggregations benefit from protection from predators because the predation risk for any one individual is reduced (Hamilton 1971). Birds can also mob predators more effectively when they are at a higher density, since there are more individuals present in a smaller area to harass intruders (Phillips 1998; Clode 1993; Hernández-Matías et al. 2003). Where a nest is located in a colony also has an important effect on breeding success, since birds that nest on the edge of a colony are more accessible and therefore more susceptible to terrestrial predators (Minias and Kaczmarek 2013). Nests on the edge of a colony tend to be in poorer habitat than those in the centre, since the centre areas are first occupied by older, more experienced individuals (Léger and McNeil 1987; Minias and Kaczmarek 2013).

The density and location of nests in a colony can affect aggressive behaviours, since these behaviours are tied to territoriality and the closeness of other individuals (Spurr 1974; Vermeer et al. 1988; Côté 2000; Alonso-Alarez and Velando 2001). In areas with higher nest density, birds may compete more for resources or spend more time and energy defending their territory and protecting their young from neighbouring conspecifics (Vermeer et al. 1988; Hötker

2000; Forero et al. 2002). At the edge of a colony, the literature predicts either increased aggression towards unfamiliar individuals passing by at a colony's edge (Butler and Janes-Butler 1982) or decreased aggression since there are fewer individuals at a lower density surrounding the focal nest and less competition for lower-quality territories (Spurr 1974; Côté 2000).

Aggressive behaviours can be beneficial for territory defense, communication and increased access to food or mates, however, there may exist trade-offs between aggression and parental behaviours that could negatively impact breeding success (Hunt and Hunt 1976; Wagner et al. 2000; Pryke and Griffith 2009). At the most fundamental level, higher aggressive and territorial behaviours occur when androgen levels, such as testosterone, are higher (Ketterson et al. 1996). Higher levels of testosterone may supress parental behaviour, especially foraging behaviour (see Wingfield et al. 1987; McGlothlin et al. 2007) resulting in a predicted trade-off between high levels of aggression and high levels of parental behaviour (see Ketterson et al. 1992; Pryke and Griffith 2009). This trade-off is more often seen in males, but can exist in females, since the need for increased aggression can decrease the time budget available to provision chicks in either sex (McGlothlin et al. 2007; Rosvall 2013). A significant decrease in parental behaviour could decrease the quality or number of young produced (Duckworth 2006). Aggression can also be costly because of its high energy demands and the increased risk of injury, but aggression associated with some aspects of parental care, such as protection of young from predators or attacks from conspecifics, is likely beneficial (Côté 2000; Neat et al. 1998).

The double-crested cormorant (*Phalacrocorax auritus*) is an abundant colonial waterbird, whose high nest densities and large population makes it an ideal species in which to observe density-dependent effects and aggressive interactions. Cormorants have undergone an exponential population increase since the 1970s and are still increasing in many areas (Weseloh and Collier 1995; Dorr et al. 2014b). This increase has proved problematic for managers interested in protecting habitat or eliminating fish predation (Weseloh and Collier 1995; Hebert et al. 2005). The population increase may be due to increased food abundance, but there may be some aspect of cormorant's life history that makes them so successful (Weseloh et al. 1995). Trade-offs between aggression and parental behaviour have been well-studied in songbirds, but to my knowledge have not been studied in a colonial bird (Ketterson et al. 1992; Duckworth 2006; Mutzel et al. 2013). Double-crested cormorant experience density-dependent population regulation that affects population growth rates over time, but there is no information on how density dependent factors affect cormorants in a single breeding season (Guillaumet et al. 2014). By exploring how the colony's spatial structure, such as nest density and nest position, influence behaviour and, in turn, how behaviour influences fledging success, it is possible to determine if density-dependent population regulation is acting on a large cormorant population and to find a mechanism by which it occurs.

I examine if nest density and nest location (edge vs centre) in a colony affects the duration and frequency of aggressive behaviour at a ground-nesting colony of double-crested cormorants and, in turn, if aggression and parental behaviour affect fledging success. The predictions are that aggression will increase as density increases and for nests closer to the centre of the colony, since these effects have been seen in other species (e.g. Spurr 1974; Côté 2000; Hötker 2000; Stokes and Boersma 2000). I further explore if there is a trade-off between aggression and parental behaviours that affects reproductive success and whether there is a link between parental behaviour or aggression and fledging success. I predict that there will be a trade-off at the cormorant colony since cormorants engage in frequent aggressive behaviour in colonies and that the trade-off will affect fledging success (Wyman and Cuthbert 2015). I also predict that increased parental and decreased aggressive behaviour will be correlated with increased fledging success since cormorants have altricial young that require a high amount of parental care (Dorr et al. 2014b).

Methods

Study site

The research was done on Peninsula B at Tommy Thompson Park in Lake Ontario in Toronto, Canada (43_380N, 79_200W). Cormorants nested in the trees on Peninsula B beginning in 1990 and began to nest on the ground in 2002 (344 nests) (Jarvie et al. 1997; Taylor et al. 2011). The Toronto and Region Conservation Authority (TRCA), who managed the site, actively encouraged cormorants to nest on the ground beginning in 2008 in order to preserve the remaining tree canopy (Taylor et al. 2011). This corresponded with a steady increase in the size of the ground nesting colony (2008-2014, 1009-7799 nests) (TRCA 2009; Taylor et al. 2011; GS Fraser unpublished data). On Peninsula B, cormorants resided in a ground-nesting mixed-species colony consisting of ~1000 ring-billed gull (*Larus delawarensis*) nests, ~10 herring gull (*L. argentatus*) nests and ~200 Caspian tern (*Hydroprogne caspia)* nests as of 2014 (TRCA unpublished data). Each species nested in its own sub-colony; there were no areas where the species overlapped and there was a slight separation between each sub-colony (see Fig 1). Later in the breeding season, the sub-colonies became less distinct as recently fledged young loafed in other areas.

Data collection

Data were collected on Peninsula B at the Tommy Thompson Park from May 2nd to July 23rd 2014. Cormorants nested in several different ground-nesting sub-colonies, (Fig 1). The focal nests were divided into two categories (centre or edge) based on where they were in the observed sub-colony. Human presence in a mixed-species cormorant-gull colony reduces the nest success of cormorants, since gulls will take advantage of the disturbance to eat their eggs (see Kury and Gochfeld 1975; Duerr et al. 2007). To minimize investigator disturbance, I accessed the colony using a kayak and conducted all observations from a blind (see Fig 1).

I used 20 minute observations on edge and interior nests to measure the frequency and duration of cormorant behaviours. Observations generally began at 10:00 and ended at 15:00 (range 08:30 to 15:20). Each nest was observed once per week and to avoid bias from watching certain nests at certain times, the time each nest was observed was alternated weekly. If both members of a pair were on the nest, the adult closer to the centre of the nest was the focal bird. Two nests were always watched at once. The duration and frequency of all parental associated behaviours (such as feeding chicks or handling nesting material) and aggressive behaviours (such as lunging at another bird or calling) were recorded (Table 1) (Dorr et al. 2014 b). Behaviours were chosen based on descriptions in Dorr et al. (2014 b) and then expanded upon based on preliminary field observations taken in late April 2014. A behaviour was considered to be independent if it occurred more than 5 seconds after another behaviour, otherwise multiple behaviours were counted as one compound behaviour. The behaviours were combined into one of three types: 1) parental behaviours, 2) aggressive behaviours or 3) compound behaviours that consisted of both parental and aggressive behaviours, although only parental and aggressive behaviours were used in the analysis due to the low occurrence of compound behaviours (see

Table 1). I combined behaviours into these three categories to include even rare behaviours that otherwise would have occurred too infrequently to be statistically analyzed. Some behaviours, such as ‘handling nest material’ were designated differently depending on whether they occurred alone or as a compound behaviour, since this changed the context of the behaviour. Sometimes, the focal nest was blocked by another bird, which meant that it was not observed for the full 20 minute period. To compensate for this, all behavioural analyses were standardized using the total duration or frequency each behaviour type (parental, aggressive) was observed, divided by the total time the nest was observed. Both the duration and frequency of all aggressive and parental behaviours were analyzed.

To determine fledging success, the number of cormorant eggs and chicks were recorded whenever they were visible. However, the undulating ground and the high cormorant density made it difficult to see the number of chicks every week. For this reason, an estimate of fledging success was defined as the average of the number of chicks at the nest for last three observations when all chicks were present, divided by the maximum number of young observed during the breeding period. Chicks needed to be present at the nest for more than 28 days to be considered fledged (Dorr et al. 2014b). Chicks were not marked in order to minimize colony disturbance.

Data analysis

To determine if cormorant behaviour changed with location, I conducted spatial analyses of the nests using ArcGIS 10.1 (ESRI 2012). Using aerial photographs taken on Jun 17th 2014, I georeferenced the cormorant colony, identified the focal nests and created a point shapefile containing each nest. The georeferenced nests were qualitatively assessed for trends in the duration or frequency of aggression using a Jenks Natural Breaks format, which creates unequal categories based on the similarity of the data and is ideal for observing trends in the dataset (ESRI 2012).

Using R 3.1.3 I calculated the combined effect of density and nest location on the frequency and duration of aggressive behaviours (R Core Team 2015). Unlike the previous analysis, which determined fine-scale spatial trends in position using GPS coordinates, this analysis designated nests as either ‘edge’ or ‘centre’ nests based on their location in the colony. ‘Edge’ nests were always located right at the extreme edge of the sub-colony, near the ring-billed gull portion, while ‘centre’ nests were completely surrounded by cormorant nests. Cormorants only interact with other individuals that are within the length of the necks at their nests (average 0.38 m), therefore density was calculated by counting the number of nests within a 2.5 metre radius of each focal nest to ensure all interactions were captured (Siegel-Causey and Hunt 1986). Aggressive behaviours throughout the breeding season were summed for each focal nest and compared to density and location. The effects of position or density on aggression and the relationship between the behaviours and fledging success were calculated using Welch’s t-test and Pearson’s Correlation or Kendall’s Tau correlation analysis depending on whether or not the data could be normalized (Pearson 1895; Kendall 1938; Welch 1947; R Core Team 2015).

Results

I observed 24 nests in the centre (interior) portion of the sub-colony and 12 nests at the edge of the cormorant portion of the colony near the ring-billed gull portion (Fig 1). Nests in the centre started earlier, so observations began on May 2nd 2014, while the edge nests were first observed on May 14th 2014. No breeding cormorants abandoned their nests when accessing the blind, but cormorants loafing in and near the water would regurgitate food upon seeing me as a defense mechanism, especially later in the season (Kury and Gochfeld 1975). By travelling away from the shore and by quickly accessing the blind via a tunnel, I only caused an approximate five minute disruption each time I entered and exited the colony (3 times per week). Although I measured a total of 36 nests, only 32 nests were used in the analysis due to the difficulty in confirming their exact location and surrounding density using reference photos.

I predicted that cormorant aggression would increase when nests were located further away from the edge of the colony. Aggressive behaviours occurred for a longer duration and increased frequency in one small area at the centre of the sub-colony (mean duration=0.11, SD=0.032, mean frequency $6.0*10^{-3}$ beh/sec, SD=$8.7*10^{-4}$), but there was no clear gradient in the duration of these behaviours on the edge of the sub-colony compared to the centre (Fig 2). The frequency of aggressive behaviours was slightly higher on the edge of the sub-colony compared to the interior, but the trend was not very strong (edge mean=$4.2*10^{-3}$ beh/sec, SD=$1.2*10^{-3}$, interior mean=$3.9*10^{-3}$ beh/sec, SD=$1.2*10^{-3}$) (Fig 2b). Welch's t-tests showed no significant differences between the duration or frequency of aggressive behaviours at edge versus the centre of the sub-colony (aggression duration t=2,0, p=0.061, aggression frequency t=1.8, p=0.090). Overall, there were no strong trends showing that the duration or frequency of aggressive behaviour changed based on nest position.

High nest density was predicted to increase the duration and frequency of cormorant aggression. There was a significant relationship between nest density and position detected using a t test for homogeneity of variance, (t=-8.2, p<0.01) however, the effect of density on aggression was different from the effect on position. Density was lower for edge nests (mean density= 0.84 nests/m^2) than for centre nests (mean density =1.6 nests/m^2). Across all nests, density was significantly negatively associated with both the duration and frequency of aggressive behaviour (duration r=-0.36, p=0.043, frequency r=-0.45, p=<0.01) (Fig 3a, 3b). Since the centre of colonies are first occupied by older birds, it is important to test for density effects separate from colony position (Minias and Kazcmarerk 2013) (Fig 3c-3f). Density was significantly negatively correlated with aggression frequency at the edge of the sub-colony (r=-0.80, p<0.01) but not with aggression duration and not at the centre of the colony. Overall, the results indicate that aggression increased in areas where density is lower overall and at the edge of the sub-colony.

I examined the relationship between aggression and parental behaviour for all nests and separately for edge nests and predicted trade-offs between the behaviours. Only when the frequency or duration of aggressive behaviours overall or at the edge or the centre of the colony were significantly associated with density did I test for trade-offs, because I was only interested in trade-offs to understand mechanisms of density dependent population regulation in cormorants. Aggression duration across all nests (n=32) was significantly positively associated with the duration and frequency of parental behaviour (parental duration r=0.40, p=0.023, parental frequency r=0.40, p=0.022), (Fig 4a, 4b). The frequency of aggressive behaviour across all nests was significantly positively associated with the frequency (r=0.38, p=0.034) of parental behaviour (Fig 4c, 4d) but not the duration (r=0.22, p=0.22). For edge nests, (n=10) the frequency of aggressive behaviour was not significantly associated with the duration (r=0.19, p=0.60) or frequency (r=0.080 p=0.83) of parental behaviour (Fig 4e, 4f). Since parental behaviour either was not related to aggressive behaviour or increased as aggression increased, there was no trade-off between the two behaviour categories.

I predicted that increased fledging success would be directly correlated with decreased aggressive behaviour and increased parental behaviour. There was no significant effect of parental (Fig 5) or aggressive (Fig 6) behaviours on fledging success for all nests or for centre or edge nests.

Discussion

I examined if aggression was predicted by nest location and density, if there was a trade-off between aggressive and parental behaviours and if aggressive and parental behaviours affected fledging success. Focal nest observations did not support the prediction that aggression increased closer to the centre of the colony or with increased density. Contrary to the prediction, increased density corresponded with decreased aggression, particularly for edge nests. Similarly, aggression and parental behaviours for edge nests and overall were positively, not negatively, correlated, suggesting no trade-off between these behaviours. Equally, parental and aggressive behaviours were not associated with fledging success regardless of where the birds were located in the colony. These results do not show how density dependent controls may be acting on a cormorant colony since increased density did not affect behaviour in a way that then affected fledging success.

This research contradicts previously published literature on the relationship between aggression, density, position, parental behaviour and fledging success. For example, king penguins (*Aptenodytes patagonicus*) are more aggressive when they nest closer to the colony centre, (Côté 2000) while black-backed gulls (*L. marinus*) and Magellenic penguins (*Spheniscus magellanicus*) are more aggressive at higher densities (Butler and Trivelpiece 1981; Stokes and

Boersoma 2000) and fledging success can be negatively correlated to agonistic interactions (Butler and Janes-Butler 1982). In non-colonial nesting birds including the Western bluebird (*Sialia mexicana)* and dark-eyed junco (*Junco hyemalis*) there is a trade-off between parental and aggressive behaviour which is mediated through testosterone levels (Ketterson et al. 1992; Duckworth 2006). Limitations in the experimental design, including a low sample size or difficulty distinguishing individuals, may explain why cormorants differed from these species, however, it is likely that the biology of cormorants plays a more important role. For instance, double-crested cormorants may display different trends than other species because sex may influence behaviour. Many colonial birds, such as the crested auklet (*Aethia cristatella*) or Atlantic puffins (*Fraercula arctica*) have different rates of foraging and parental care based on sex, so knowing the sex of focal cormorants may reveal differences in behaviour (Creeleman and Storey 1991; Fraser et al. 2002). However, when studying cormorants, Léger and McNeil (1985) report few differences in parental care behaviours between sexes and other research on different cormorant species reached the same conclusion (Hatch et al. 2000).

Aggression increased when density decreased overall and for edge nests. For centre nests, aggression was not related to density, perhaps because there was a weak gradient of density in that part of the colony (1.3 to 1.9 birds/m^2). Aggression may increase at lower densities because cormorants will have a slightly larger territory, so they may need to expend more effort to defend it. Wyman and Cuthbert (2015) found that nest location was more important for behavioural interactions than nest density among double-crested cormorants, but they did not find the same negative effect that I observed.

Cormorant aggression was generally not affected by colony position, despite the fact that position was highly related to density, and density did affect aggression. This may be because individuals nesting in the centre usually interact with only their neighbours and the occasional passerby, while individuals nesting at the colony's edge experience continual interactions with loafing conspecifics, increasing aggression despite the lower density. The cormorant-sub colony edge was bordered by a ring-billed gull sub-colony, which may have increased interspecific interactions since birds in mixed-species colonies respond differently to heterospecifics compared to conspecifics (Ellis and Good 2006; Somers et al. 2011; Wyman and Cuthbert 2015). However, in this study, ring-billed gulls never instigated interactions with cormorants because their smaller size put them at a disadvantage, so the presence of heterospecifics was unlikely the driver of the observed trend.

The duration and frequency of cormorant parental behaviours increased as aggressive behaviours increased. This may have occurred due to individual variation in birds: some individuals may be more active overall than others, so all types of behaviour would increase. For instance, older, more experienced cormorants are better at nest defense, perhaps due to increased interactions with conspecifics or increased effectiveness of each behaviour (Dorr et al. 2014b). The same effect may also carry over to parental behaviours, since older birds tend to be better parents due to factors such as experience and increased fitness benefits (Curio 1983). Some aggressive behaviours may have also been parentally motivated if cormorants were defending their young from conspecifics (Montgomerie and Weatherhead 1988). For example, increased eggs or chicks may result in increased parental behaviours and these individuals may also have higher aggression because they have more young to defend (Montgomerie and Weatherhead 1988). It was not possible to measure precisely how many eggs or chicks each cormorant nest contained, since entering the cormorant colony can cause nest abandonment, so this could not be verified.

Neither aggressive nor parental behaviours appeared to have affected fledging success. There are several possible explanations for this. First, external, random factors such as predation, timing of laying (Pratt and Winkler 1985) or extreme weather may have been more important than behaviour or nest density (Cuthbert et al. 2002; Mallory et al. 2009; Dorr et al. 2014a). Some species, such as tropical passerines, experience high predation rates, so the time spent caring for the young does not result in high fledging success (Robinson et al. 2000). However, despite the presence of coyotes and raccoons at this site, predation in the cormorant colony was not observed during the study and no focal nests were lost to predation. Second, the variation in fledging success was quite low and only one nest failed since the eggs did not hatch. Third, fledging success may have been overestimated since the measure of fledging success did not include the number of eggs in each nest and because chicks were considered fledged when they left the nest and began loafing. Other factors that affect colonies, such as food depletion, are likely not a factor at this site because Lake Ontario can support a large population of birds due to its size (Birt et al. 1987; Forero et al. 2002) and cormorants have not yet reached carrying capacity at TTP (see chapter 1) (Jarvie et al. 1997).

Cormorant population was likely not being regulated by density at the ground-nesting colony at TTP. Cormorant populations in North America are at some of their highest levels ever recorded in history primarily due to increased food resources (Weseloh and Collier 1995; Dorr et al. 2014b). In this study, nests were spaced farther apart than the minimum comfortable distance between them denoted by the length in their necks, indicating that there may still be room for density to increase, and in fact, density has increased at this site since at least 2005 (TRCA 2014). In other colonies on the Great Lakes, density dependent effects have reduced cormorant colony growth rates over time (Guillaumet et al. 2014). Since no culling occurs at TTP, it is an ideal location to continue studying the relationship between density, position, behaviour and fledging success without the results being confounded by lethal control. Future research at TTP could involve studying the changes in density-dependent effects on population over multiple years by experimentally manipulating nest structure by moving nests or adding woody debris (Guillaumet et al. 2014).

Literature Cited

Alonso-Alvarez C, Velando A. 2001. Effect of testosterone on the behaviour of yellow-legged gulls (*Larus cachinnans*) in a high-density colony during the courtship period. Etho. Ecol. Evol. 13(4): 341-349.

Ashoori A, Barati A. 2013. Breeding success of Black-crowned Night Heron (*Nycticorax nycticorax*), Little Egret (*Egretta garzetta*) and Cattle Egret (*Bubulcus ibis*) (Aves: *Ardeidae*) in relation to nest height in the South Caspian Sea. Ital. J. Zool. 80(1): 149-154.

Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Mar. Ecol-Prog Ser. 40(1): 205-208.

Burger J. 1983. Grebes nesting in gull colonies: protective associations and early warning. Am Nat. 123(3): 327-337.

Butler RG, Janes-Butler S. 1982. Territoriality and behavioural correlates of reproductive success of great black-backed gulls. Auk. 99(1): 58-66.

Butler RG, Trivelpiece W. 1981. Nest spacing, reproductive success, and behavior of the great-black backed gull (*Laurs marinus*) Auk. 98(1): 99-107.

Clode D. 1993. Colonially breeding seabirds: predators or prey? Trends Ecol. Evol. 8(9): 336-338.

Côté SD. 2000. Aggressiveness in king penguins in relation to reproductive status and territory location. Anim Behav. 59(4): 813-821.

Creelman, E, Storey AE. 1991. Sex differences in reproductive behavior of Atlantic Puffins. Condor 93(2): 390-398.

Curio E. 1983. Why do young birds produce less well? Ibis. 125(3): 400-404.

Cuthbert FJ, Wires LR, McKearnan JE. 2002. Potential impacts of nesting double-crested cormorants on great blue herons and black-crowned night-herons in the U.S. Great Lakes region. J Great Lakes Res. 28(2):145-154.

Danchin E, Wagner RH. 1997. The evolution of coloniality: the emergence of new perspectives. Trends Ecol. Evol. 12(9): 342-347.

Dorr BS, Hanson-Dorr KC, DeVault TL, Guillaumet A, Barras SC. 2014a. Geographic segregation and evidence of density-dependent changes in sex rations in an abundant colonial waterbird. Integr. Zool. 9(5): 570-582.

Dorr BS, Hatch JJ, Weseloh DV. 2014b. Double-crested Cormorant (*Phalacrocorax auritus*), The Birds of North America Online (A. Poole, Ed.). [Internet] [cited 2015 04 Jul] Ithaca: Cornell Lab of Ornithology; Available from: http://bna.birds.cornell.edu/bna/species/441

Duckworth RA. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. Behav Ecol. 17(6):1011-1019.

Duerr AE, Donovan TM, Capen DE. 2007. Management-induced reproductive failure and breeding dispersal in double-crested cormorants on Lake Champlain. J Wildl Manage. 71(8):2565-2574.

Ellis JC. Good TP. 2006. Nest attributes, aggression, and breeding success of gulls in single and mixed species subcolonies. Condor. 108(1): 211-219.

ESRI 2012. ArcMap 10.1 Build 3035. Redlands CA: Environmental Systems Research Institute.

Forero MG, Tella JL, Hobson KA, Bertellotti M, Blanco G. 2002. Conspecific food competition explains variability in colony size: a test in Magellanic penguins. Ecology. 83(12): 3466-3475.

Fraser GS, Jones IL, Hunter FM. 2002. Male-female differences in parental care in monogamous crested auklets. Condor. 104(2): 413-423.

Guillaumet A, Dorr BS, Wang G, Doyle TJ. 2014. The cumulative effects of management on the population dynamics of the Double-crested Cormorant *Phalacrocorax auritus* in the Great Lakes. Ibis 156(1):141-152.

Hamilton WD. 1971. Geometry for the selfish herd. J. Theor. Biol. 31(1): 295-311.

Hatch JJ, Brown KM, Hogan GG, Morris RD. 2000. Great Cormorant (*Phalacrocorax carbo*), The Birds of North America Online (A. Poole, Ed.). [Internet] [cited 2015 21 Aug] Ithaca: Cornell Lab of Ornithology; Available from: http://bna.birds.cornell.edu/bna/species/553

Hebert CE, Duffe J, Weseloh CDV, Senese TEM, Haffner DG. 2005. Unique islands habitats may be threatened by double-crested cormorants. J Wildlife Manage. 69(1): 68-76.

Hernández-Matías A, Jover L, Ruiz, X. 2003. Predation on common tern eggs in relation to sub-colony size, nest aggregation and breeding synchrony. Waterbirds. 26(3): 280-289.

Hötker H. 2000. Intraspecific variation in size and density of Avocet colonies: effects of nest-distances on hatching and breeding success. J. Avian Biol. 31(3) 387-398.

Hunt GL Jr, Hunt MW. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology. 57(1): 62-75.

Jarvie S, Blokpoel H and Chipperfield D. 1997. A Geographic Information System To Monitor Nest Distributions of Double-Crested Cormorants and Black-Crowned Night-Herons at Shared Colony Sites Near Toronto, Canada. Symposium on Double-Crested Cormorants: Population Status and Management Issues in the Midwest. Paper 13. Available from http://digitalcommmons.unl.edu/nwrccormorants/13

Jovani R. Grimm V. 2008. Breeding synchrony in colonial birds: from local stress to global harmony. P. Roy. Soc. B. 275(1642):1557-1563.

Kendall M. 1938. A New Measure of Rank Correlation. Biometrika. 30(1–2): 81–89.

Ketterson ED, Nolan V Jr, Wolf L, Ziegenfus C. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). Am Nat. 140(6): 980-999.

Ketterson ED, Nolan V Jr., Cawthorn MJ, Parker PG, Ziegenfus C. 1996. Ibis. Phenotypic engineering: using hormones to explore the mechanistic and functional bases of phenotypic variation in nature. Ibis. 138(1) 70–86.

Kury CR and Gochfeld M. 1975. Human interference and gull predation in cormorant colonies. Biol. Conserv. 8(1): 23-34.

Léger C, McNeil R. 1985. Nest attendance and care of young in double-crested cormorants. Colon. Waterbird. 8(2): 96-103.

Léger C, McNeil R. 1987. Choix de l'emplacement des nids de cormorans à aigrettes (*Phalacrocorax auritus*) aux îles de la Madeleine, Québec. Can. J. Zool. 65(1):24-34.

Liordos V, Lauder AW. 2015. Factors affecting nest success of tufted ducks (*Aythya fuligula*) nesting in association with black-headed gulls (*Larus ridibundus*) at Loch Leven, Scotland. Waterbirds. 38(2):208-213.

Mallory ML, Gaston AJ, Forbes MR, Gilchrist HG. 2009. Influence of weather on reproductive success of northern fulmars in the Canadian high arctic. Polar Biol. 32(4):529-538.

McGlothlin JW, Jawor JM, Ketterson ED. 2007. Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. Am Nat. 170(6): 864-875.

Minias P, Kaczmarek K. 2013. Is it always beneficial to breed in the centre? trade-offs in nest site selection within the colony of a tree-nesting waterbird. J. Ornithol. 154(4):945-953.

Montgomerie RD, Weatherhead PJ. Risks and rewards of nest defence by parent birds. Q Rev. Bio. 63(2): 167-187.

Mutzel A, Blom MPK, Spagopoulou F, Wright J, Dingemanse NJ, Kempenaers B. 2013. Temporal trade-offs between nestling provisioning and defence against nest predators in blue tits. Anim. Behav. 85(6):1459-1469.

Neat FC, Taylor AC, Huntingford FA. 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. Anim Behav. 55(4): 875-882.

Pearson K. 1895. Notes on regression and inheritance in the case of two parents. P. R. Soc. London. 58(1): 240–242.

Phillips RA, Furness RW, Stewart FM. 1998. The influence of territory density on the vulnerability of arctic skuas *Stercorarius parasiticus* to predation. Biol Conserv. 86(1): 21-31.

Pratt HM, Winkler DW. 1985. Clutch Size, Timing of Laying, and Reproductive Success in a Colony of Great Blue Herons and Great Egrets. Auk. 102(1): 49-63.

Pryke SR, Griffith SC. 2009. Socially mediated trade-offs between aggression and parental effort in competing color morphs. Am. Nat. 174(4): 455-464.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org/.

Robinson WD, Robinson TR, Robinson SK, Brawn JD. 2000. Nesting success of understory forest birds in central Panama. J. Avian Biol. 31(2): 151-164.

Rolland C, Danchin E, de Fraipont M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Am. Nat. 151(6): 514-529.

Rosvall KA. 2013. Life history trade-offs and behavioral sensitivity to testosterone: An experimental test when female aggression and maternal care co-occur. PLoS ONE.8(1).

Siegel-Causey D, Hunt GL. Jr. 1986. Breeding-site selection and colony formation in double-crested and pelagic cormorants. Auk. 103(1): 230-234.

Somers CM, Doucette JL, Weseloh DVC, Kjoss VA and Brigham RM. 2011. Interactions between double-crested cormorants and other ground-nesting species. Waterbirds. 34(2): 168-176.

Spurr EB. 1974. Individual differences in aggressiveness of adelie penguins. Anim Behav. 22(3): 611-616.

Stokes DL, Boersma PD. 2000. Nesting density and reproductive success in a colonial seabird, the magellanic penguin. Ecology. 81(10): 2878-2891.

Taylor B, Andrews D, Fraser GS. 2011. Double-crested cormorants and urban wilderness: conflicts and management. Urban Ecosyst. 14(3):377-394.

[TRCA 2009] The Toronto and Region Conservation Authority Index to Authority Meeting #2/09. 2009. [Internet] [cited 2015 Apr 15] Available from: http://tommythompsonpark.ca/global/pdfs/AuthorityAgenda02-09-March27_2009.pdf

[TRCA 2014] Management of colonial waterbirds at Tommy Thompson Park. Cormorant Advisor Group Meeting #12. 2014.

Vermeer K, Power D, Smith JGE. 1988. Habitat selection nesting biology of roof-nesting glaucous-winged gulls. Colon. Waterbird. 11(2): 189-201.

Wagner RH, Danchin E, Boulinier T, Helfenstein F. 2000. Colonies as byproducts of commodity selection. Behav. Ecol. 11(5): 572-573.

Welch BL. 1947. The generalization of "Student's" problem when several different population variances are involved". Biometrika 34(1–2): 28–35.

Weseloh DV, Collier B. 1995. The rise of the double-crested cormorant on the Great Lakes: Winning the war against contaminants. Environment Canada. 12 p.

Weseloh DV, Ewins PJ, Stuger J, Mineau P, Bishop CA, Postupalsky S, Ludwig JP. 1995. Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproductive output between 1913 to 1991. Colon. Waterbirds. 18(1): 48-59.

Wingfield JC, Ball GF, Dufty AM Jr., Hegner RE, Ramenofsky M. 1987. Testosterone and aggression in birds. American Sci. 75(6): 602-608.

Wyman KE, Cuthbert FJ. 2015. Species Identity and Nest Location Predict Agonistic Interactions at a Breeding Colony of Double-Crested Cormorants (*Phalacrocorax auritus*) and Great Blue Herons (*Ardea herodias*). Waterbirds. 38(2): 201-207.

Tables

Table 1: The sum of the duration (sec) and frequency of different behaviours displayed by 32 focal ground-nesting cormorants (108 hours of observation) on Peninsula B of Tommy Thompson Park, from May 2nd to July 23rd 2014. The type of behaviour designates it as an aggressive, parental or both behaviour for the subsequent analyses.

Behaviour	**Type**	**Total duration (sec)**	**Total frequency**
Calling	Aggressive	314	75
Lunging	Aggressive	4752	881
Charging	Aggressive	3	1
Pecking	Aggressive	3	1
Handling Nest Material and Calling	Aggressive	1674	46
Handling Nest Material and Lunging	Aggressive	16819	460
Handling Nest Material and Lunging and Calling	Aggressive	4070	62
Calling and Lunging	Aggressive	409	29
Lunging and Charging	Aggressive	5	1
Lunging and Pecking	Aggressive	13	2
Handling Nest Material	Parental	11927	754
Feeding Young	Parental	1326	125
Handling Nest Material and Feeding Young	Parental	105	3
Calling and Lunging and Feeding Young	Both	55	1
Calling and Feeding Young	Both	10	1
Lunging and Feeding Young	Both	146	6

Figures

Figure 1: Aerial view of the ground-nesting double-crested cormorant colony on Peninsula B of Tommy Thompson Park in 2014 with the area circled showing where all focal nests were located. Two sub-colonies of double-crested cormorants are visible in this image, as well as one of the ring-billed gull sub-colonies.

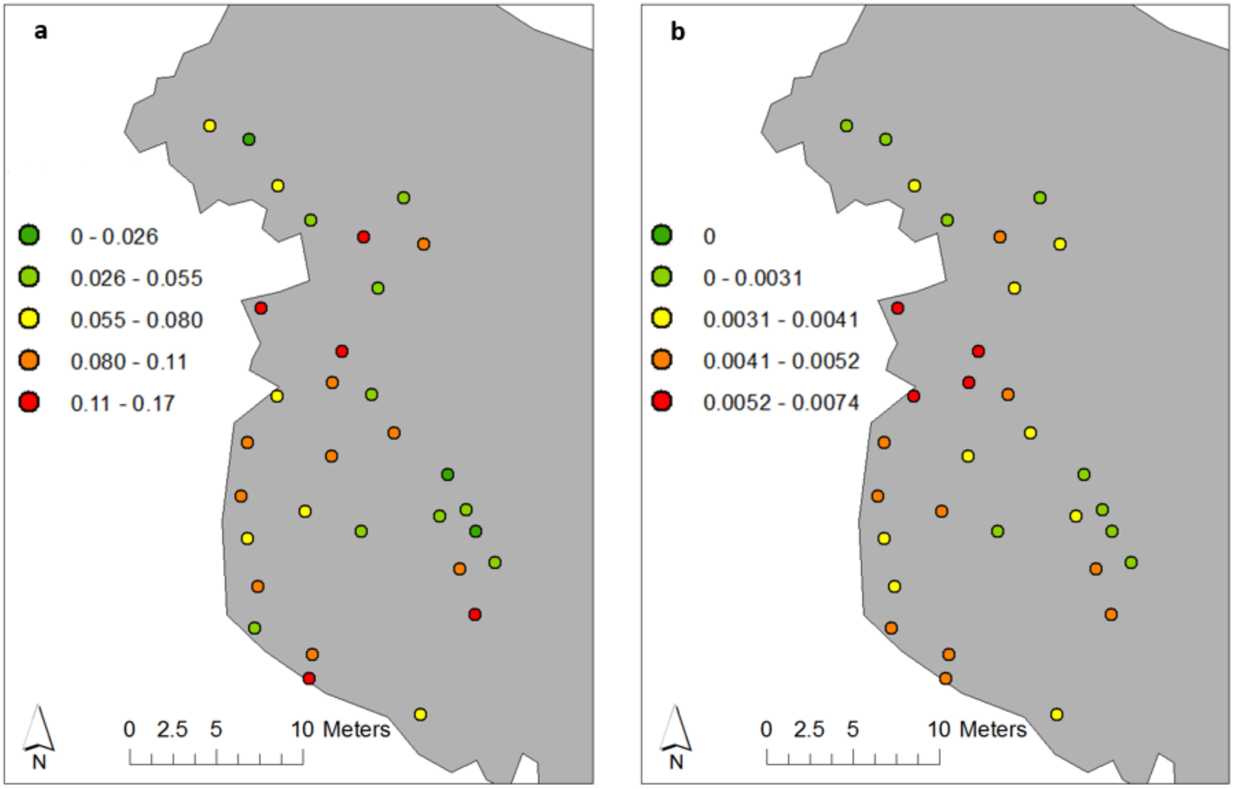


Figure 2: The duration (2a) (duration of aggressive behaviours/total time observed) and frequency (# of observations/sec) (2b) of aggressive behaviours observed for 32 double-crested cormorant focal nests on Peninsula B of Tommy Thompson Park. The area in grey is the area occupied by one cormorant sub-colony (non-focal nests are not shown).

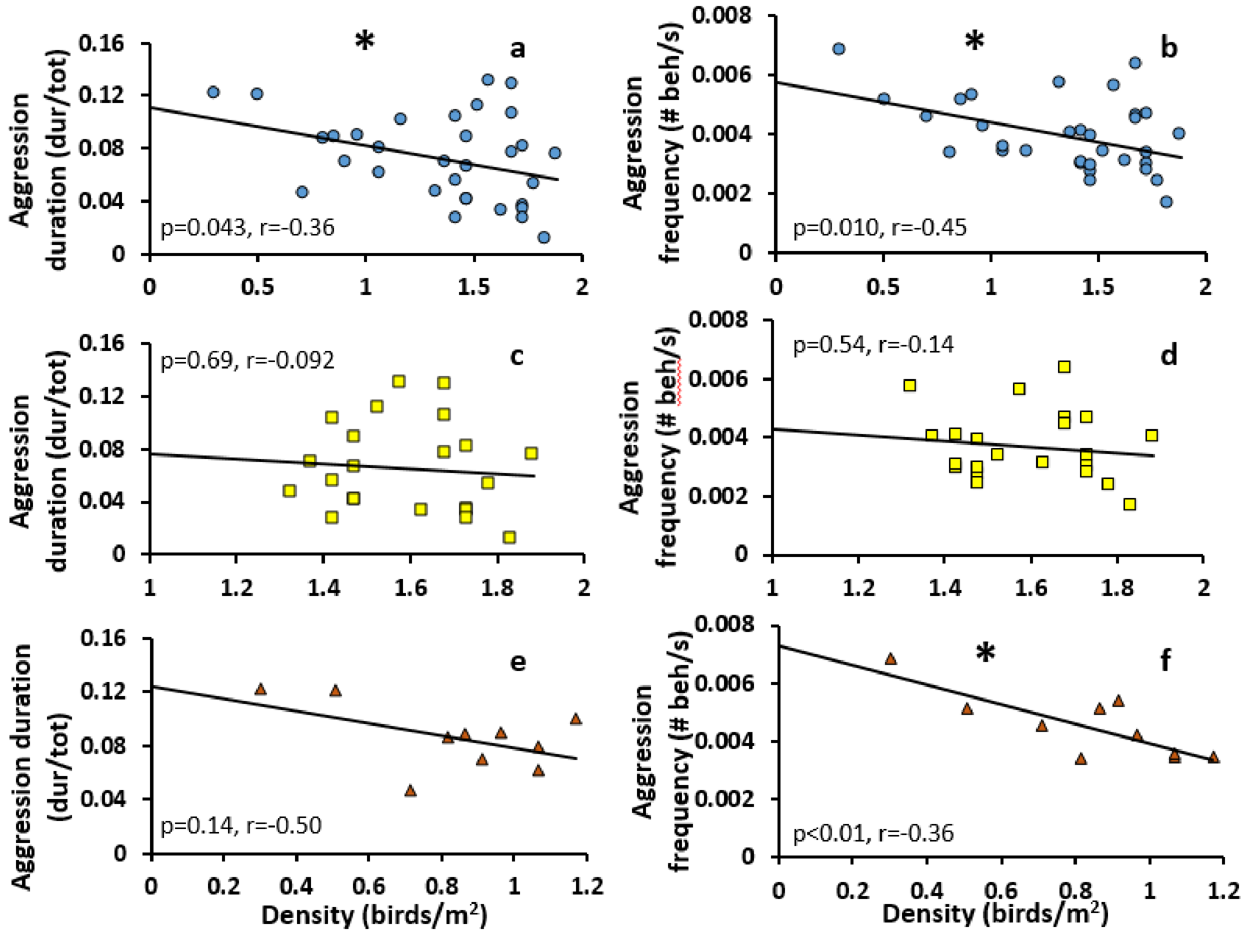
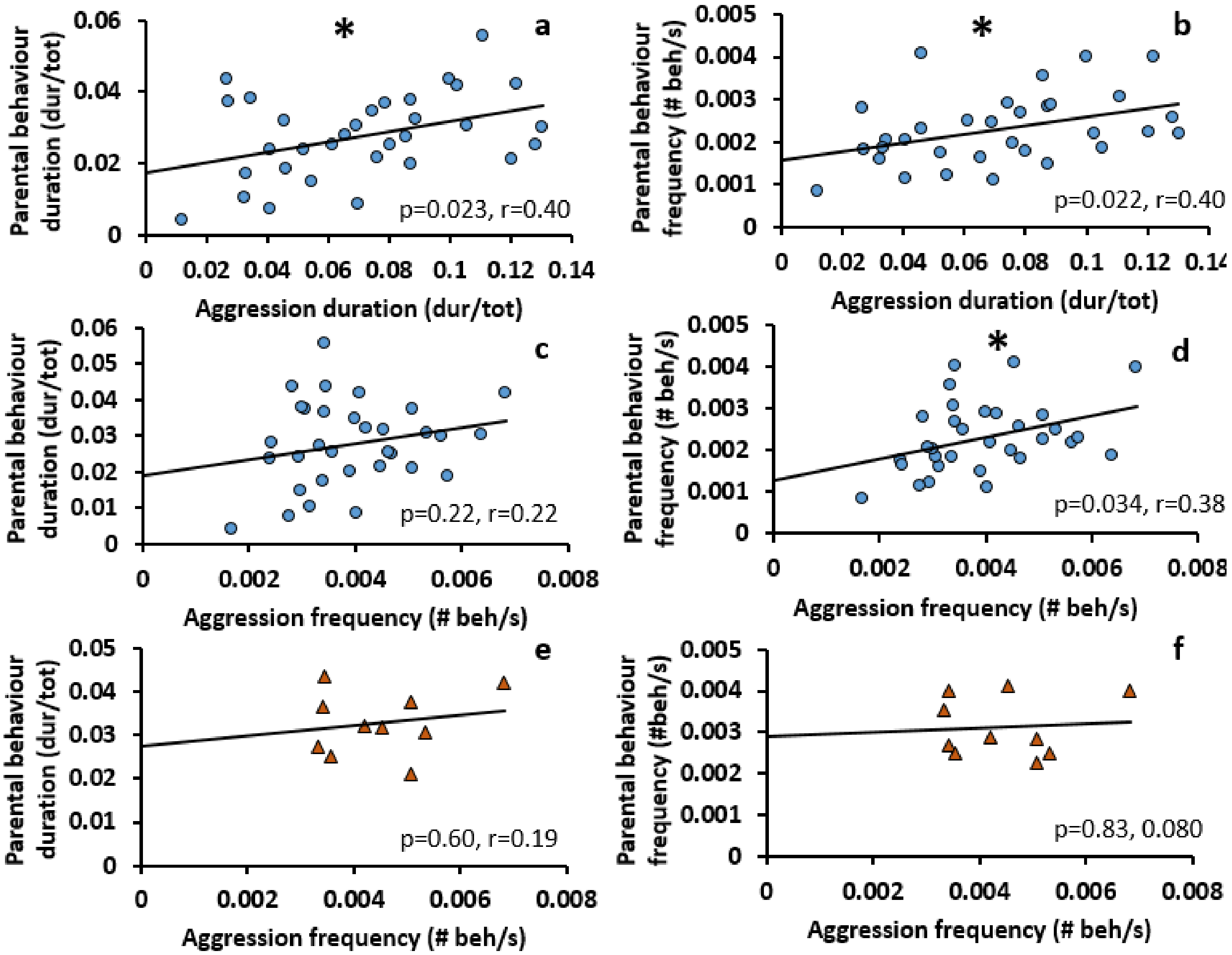


Figure 3: The relationship between the duration or frequency of aggressive behaviours and density for ground-nesting double-crested cormorant focal nests at Tommy Thompson Park. Figures 3a and 3b show the duration (duration of aggressive behaviours/total time observed) and frequency respectively of aggressive behaviours for all focal nests, figures 3c and 3d respectively show the duration and frequency of aggressive behaviours for centre focal nests and figures 3e and 3f show the duration and frequency respectively for nests located at the edge of the sub-colony. Graphs with a star indicate a significant relationship ($p<0.05$).



<u>Figure 4</u>: The relationship between parental and aggressive behaviour for ground-nesting double-crested cormorant focal nests at Tommy Thompson Park. Figures 4a and 4b show the relationship between parental behaviour duration (duration of parental behaviours/total time observed) or parental behaviour frequency (behaviours/sec) and aggression duration, respectively for all focal nests, while figures 4c and 4d show the relationship between parental behaviour duration or frequency respectively, and aggression frequency for all focal nests. Figures 4e and 4f show the relationship between parental behaviour duration or frequency and aggression frequency, respectively, for all edge focal nests. Graphs with a star indicate a significant relationship ($p<0.05$).

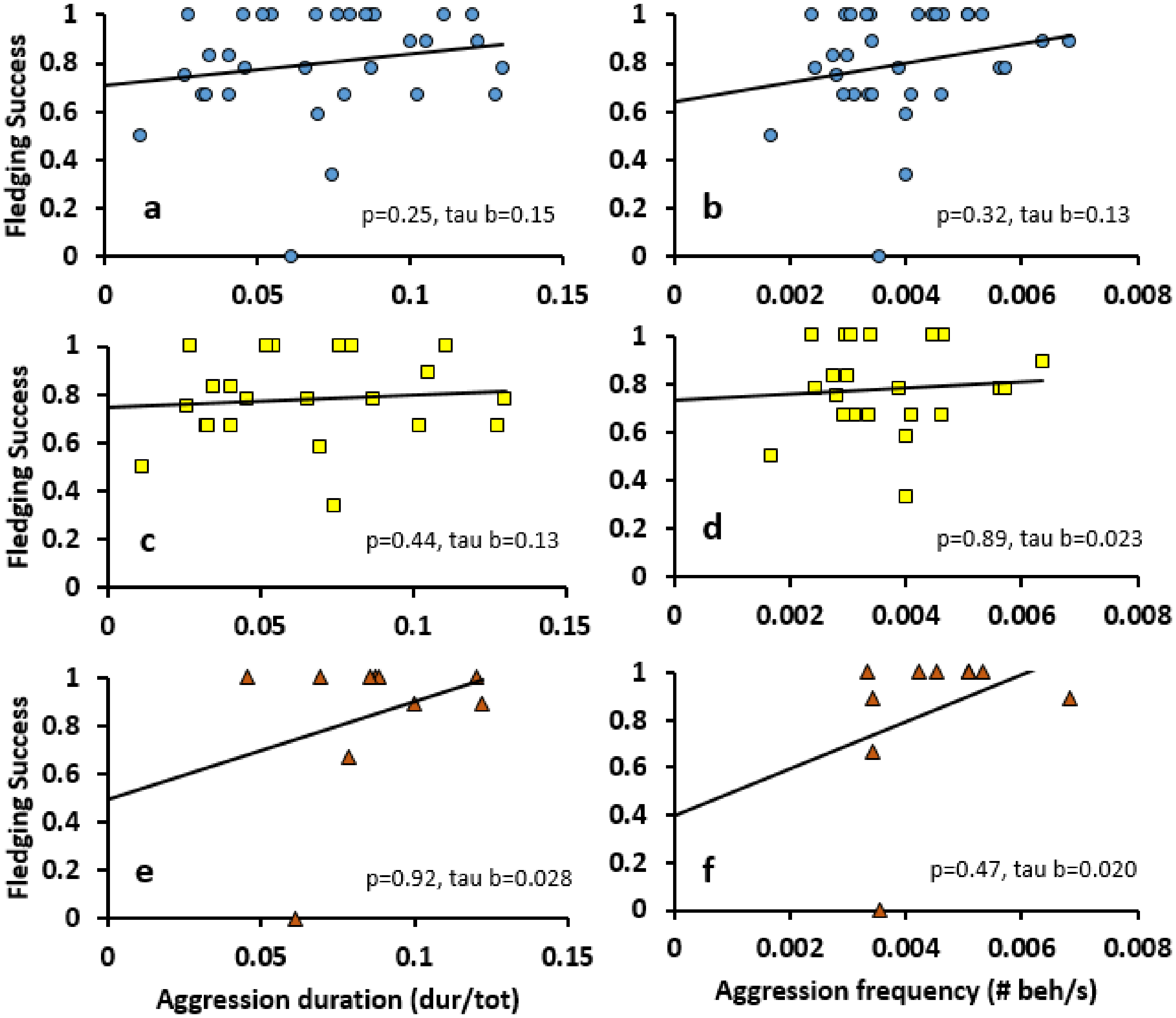


Figure 5: The relationship between fledging success of double-crested cormorant focal nests in a ground nesting colony at Tommy Thompson Park and aggression duration (duration of aggressive behaviours/total time observed) or frequency (behaviours/sec) for all nests (Fig 5a, 5b), centre nests (Fig 5c, 5d) and edge nests (Fig 5e, 5f) or frequency. A star above the graph indicates the relationship is significant ($p<0.05$).

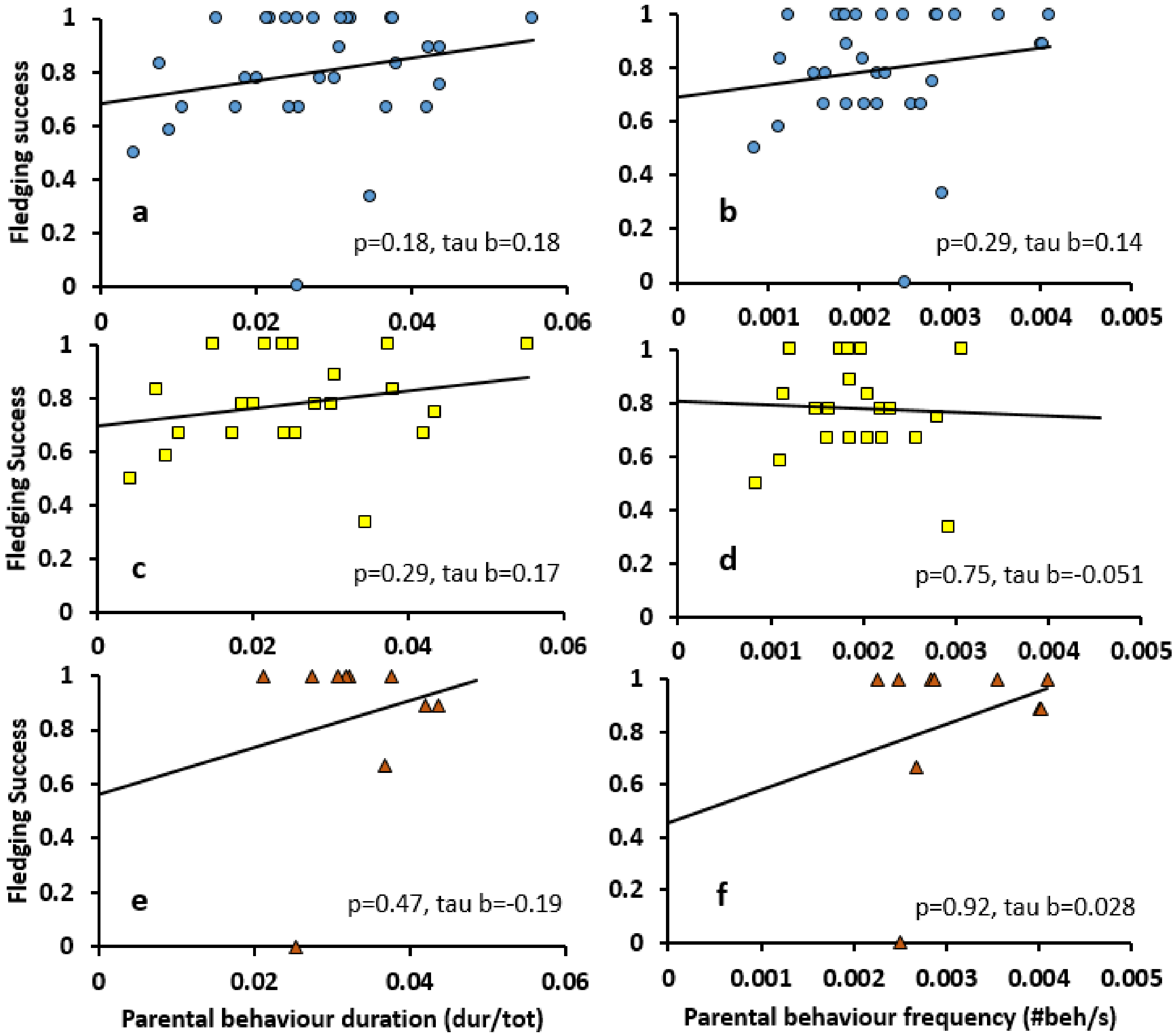


Figure 6: The relationship between fledging success of double-crested cormorant focal nests in a ground nesting colony at Tommy Thompson Park and parental behaviour duration (duration of parental behaviours/total time observed) or frequency (behaviours/sec) for all nests (Fig 6a, 6b), centre nests (Fig 6c, 6d) and edge nests (Fig 6e, 6f) or frequency. A star above the graph indicates the relationship is significant ($p<0.05$).

Conclusion

Many different interest groups, including managers, biologists and industry are interested in cormorants to aid in management or conservation. The threat cormorants may pose to fisheries and habitat creates pressure to cull them, while their adaptability and large population increase makes them interesting and easy birds to study (Weseloh and Collier 1995; Hebert et al. 2005; Dorr et al. 2010; but see Wires 2015). To address whether cormorants warrant their negative reputation in respect to their effect on other waterbirds, I examined if cormorants nesting in a mixed-species colony with black-crowned night herons caused heron decline by observing indirect and direct interactions, such as spatial patterns in their nest position and nest usurpation. To examine whether density dependence affected cormorant populations and to understand more about cormorant life-history, I also analyzed whether cormorants in a ground-nesting colony changed the duration or frequency of their aggressive behaviour in response to colony position or density and if aggressive and parental behaviours affected fledging success. Although very different, the intention of both projects was to understand more about the factors that affect cormorant interactions, whether between conspecifics or heterospecifics and provide insight to guide management decisions. As a result, I was able to compare the differences in interactions and colony spatial structure that occurs in mixed and single-species colonies and in ground and tree nesting colonies and explore aspects of cormorant life history, including why they are so successful.

The research on cormorant interactions in mixed-species colonies can be extended to other colonies and contributes to the ongoing dialogue on whether cormorants affect herons (see Shieldcastle and Martin 1997; Skagen et al. 2001; Cuthbert et al. 2002; Weseloh et al. 2002) and provides information to guide management decisions. My results act as a microcosm of the current research, since cormorants affected herons in some areas but not others. Because cormorants had a different effect on herons on both peninsulas, despite them being so close together, it highlights the variance that can occur even in a small area and the importance of studying cormorants at the sub-colony scale. Since there may be small variations in the effect of cormorants at different scales, management may only need to be applied to a small area in order to decrease their effect.

My research on cormorant behaviour in a single-species colony provides a more nuanced view on their breeding biology and the factors that affect it. Cormorants may have been so successful at increasing their population because they are more affected by external factors such as fish populations rather than intrinsic factors, since no behaviours affected fledging success (Wesleoh and Collier 1995). Therefore, it may be necessary to control cormorants by limiting their access to resources or by directly culling them, rather than expecting the population to self-regulate.

General Introduction and Conclusion Literature Cited

Ashmole. NP. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b(3): 458-473.

Baldi R, Campagna C, Pedraza S, Le Boeuf BJ. 1996. Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. Anim Behav. 51(4): 717-724.

Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA. 1987. Ashmole’s halo: direct evidence for prey depletion by a seabird. Mar. Ecol. Prog. Ser. 40(1): 205-208.

Brown CR, Brown MB. 1987. Group-living in cliff swallows as an advantage in avoiding predators. Behav Ecol Sociobiol. 21(2): 97-107.

Brown KM, Lang AS. 1996. Cannibalism by color-banded ring-billed gulls. Colon. Waterbirds. 19(1): 121-123.

Burger J. 1983. Grebes nesting in gull colonies: protective associations and early warning. Am Nat. 123(3): 327-337.

Clode D. 1993. Colonially breeding seabirds: predators or prey? Trends Ecol. Evol. 8(9): 336-338.

Coulson JC. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature. 217(5127): 478-479.

Craig EC, Elbin SB, Danoff-Burg JA, Palmer MI. 2012. Impacts of double-crested cormorants (Phalacrocorax auritus) and other colonial nesting waterbirds on plant and arthropod communities on islands in an urban estuary. Waterbirds. 35(Special Publication 1): 4-12.

Cuthbert FJ, Wires LR, McKearnan JE. 2002. Potential impacts of nesting double-crested cormorants on great blue herons and black-crowned night-herons in the U.S. Great Lakes region. J Great Lakes Res. 28(2): 145-154.

Danchin E, Wagner RH. 1997. The evolution of coloniality: the emergence of new perspectives. Trends Ecol. Evol. 12(9): 342-347.

Dorr BS, Aderman T. Butchko PH, Barras SC. 2010. Management effects on breeding and foraging numbers and movements of double-crested cormorants in the Les Cheneaux Islands, Lake Huron, Michigan. J. Great Lakes Res. 36(2): 224-231.

Dorr BS, Hatch JJ, Weseloh DV. 2014a. Double-crested Cormorant (*Phalacrocorax auritus*), The Birds of North America Online (A. Poole, Ed.). [Internet] [cited 2015 04 Jul] Ithaca: Cornell Lab of Ornithology; Available from: http://bna.birds.cornell.edu/bna/species/441

Dorr BS, Hanson-Dorr KC, DeVault TL, Guillaumet A, Barras SC. 2014b. Geographic segregation and evidence of density-dependent changes in sex rations in an abundant colonial waterbird. Integr. Zool. 9(5): 570-582.

Dorr BS, Somers C. 2012. The direction of research and management of double-crested cormorants heading into the 2000s: symposium overview and future information needs. Waterbirds. 35(1): 138-148.

Ellis JC. Good TP. 2006. Nest attributes, aggression, and breeding success of gulls in single and mixed species subcolonies. Condor. 108(1): 211-219.

Forero MG, Tella JL, Hobson KA, Bertellotti M, Blanco G. 2002. Conspecific food competition explains variability in colony size: a test in Magellanic penguins. Ecology. 83(12): 3466-3475.

Fritz, Trillmich KGK. 1984. The mating systems of pinnipeds and marine iguanas: Convergent evolution of polygyny. Biol J Linn Soc. 21(1-2): 209-216.

García GO, Riechert J, Favero M, Becker PH. 2014. Stealing food from conspecifics: Spatial behavior of kleptoparasitic common terns *Sterna hirundo* within the colony site. J. Ornithol. 155(3): 777-783.

Gorski W and Pajkert Z. 1997. Interactions between cormorants *Phalacrocorax carbo* and herring gulls *Larus argentatus* in their common breeding sites. Pol. J. Ecol. 45(1): 161-164.

Guillaumet A, Dorr BS, Wang G, Doyle TJ. 2014. The cumulative effects of management on the population dynamics of the Double-crested Cormorant *Phalacrocorax auritus* in the Great Lakes. Ibis 156(1):141-152.

Hatch JJ, Brown KM, Hogan GG, Morris RD. 2000. Great Cormorant (*Phalacrocorax carbo*), The Birds of North America Online (A. Poole, Ed.). [Internet] [cited 2015 21 Aug] Ithaca: Cornell Lab of Ornithology; Available from: http://bna.birds.cornell.edu/bna/species/553

Hebert CE, Duffe J, Weseloh CDV, Senese TEM, Haffner DG. 2005. Unique islands habitats may be threatened by double-crested cormorants. J Wildlife Manage. 69(1): 68-76.

Hernández-Matías A, Jover L, Ruiz, X. 2003. Predation on common tern eggs in relation to sub-colony size, nest aggregation and breeding synchrony. Waterbirds. 26(3): 280-289.

Hoi H, Hoi C, Kristofik J, Darolova A. 2002. Reproductive success decreases with colony size in the European bee-eater. Ethol. Ecol. Evol. 14(2): 99-110.

Hötker H. 2000. Intraspecific variation in size and density of Avocet colonies: effects of nest-distances on hatching and breeding success. J. Avian Biol. 31(3): 387-398.

Hunt GL Jr, Hunt MW. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology. 57(1): 62-75.

Jarvie S, Blokpoel H and Chipperfield D. 1997. A geographic information system to monitor nest distributions of double-crested cormorants and black-crowned night-herons at shared colony sites near Toronto, Canada. Symposium on Double-Crested Cormorants:

Population Status and Management Issues in the Midwest. Paper 13. Available from: http://digitalcommmons.unl.edu/nwrccormorants/13

Jovani R. Grimm V. 2008. Breeding synchrony in colonial birds: from local stress to global harmony. P. Roy. Soc. B. 275(1642): 1557-1563.

Neat FC, Taylor AC, Huntingford FA. 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. Anim Behav. 55(4): 875-882.

Pius SM, Leberg PL. 1997. Aggression and nest spacing in single and mixed species groups of seabirds. Oecologia. 111(1): 144-150.

Racine F, Giraldeau LA, Patenaude-Monette M, Giroux, JF. 2012. Evidence of social information on food location in a ring-billed gull colony, but the birds do not use it. Anim. Behav. 84(1): 175-182.

Ramos JA. 2003. Intraspecific aggression by roseate tern adults on chicks in a tropical colony. Waterbirds. 26(2): 160-165.

Rolland C, Danchin E, de Fraipont M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Am. Nat. 151(6): 514-529.

Schjørring S, Gregersen J, Bregnballe T. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. Anim. Behav. 57(3): 647-654.

Shieldcastle MC and Martin L. 1997. Colonial waterbird nesting on West Sister Island National Wildlife Refuge and the arrival of double-crested cormorants. Paper presented at: Symposium on double-crested cormorants: population status and management issues in the Midwest. 12p.

Skagen SK, Melcher CP, Muths E. 2001. The interplay of habitat change, human disturbance and species interactions in a waterbird colony. Am. Midl. Nat. 145(1): 18-28.

Somers CM, Lozer MN, Quinn JS. 2007. Interactions between double-crested cormorants and herring gulls at a shared breeding site. Waterbirds. 30(2): 241-250.

Somers CM, Doucette JL, Weseloh DVC, Kjoss VA and Brigham RM. 2011. Interactions between double-crested cormorants and other ground-nesting species. Waterbirds. 34(2): 168-176.

Szpak P, Longstaffe FJ, Millaire J-F, White CD. 2012. Stable isotope biogeochemistry of seabird guano fertilization: results from growth chamber studies with maize (*Zea Mays*). PLoS ONE 7(3). Available from:doi:10.1371/journal.pone.0033741.

Tinbergen N. 1953. Social behavior in animals. Methuen, London.

Valera F, Casas-Criville A, Hoi H. 2003. Interspecific parasite exchange in a mixed colony of birds. J. Parasitol. 89(2): 245-250.

Varela SAM, Dancin É, Wagner RH. 2007. Does predation select for or against avian coloniality? A comparative analysis. J. Evol. Biol. 20(4): 1490-1503.

Wagner RH, Danchin E, Boulinier T, Helfenstein F. 2000. Colonies as byproducts of commodity selection. Behav. Ecol. 11(5): 572-573.

Ward P, Zahavi A. 1973. The importance of certain assemblages of birds as "information-centres" for food finding. Ibis. 115(4): 517-534.

Weseloh DV, Collier B. 1995. The rise of the double-crested cormorant on the Great Lakes: Winning the war against contaminants. Environment Canada. 12 p.

Weseloh DV, Ewins PJ, Stuger J, Mineau P, Bishop CA, Postupalsky S, Ludwig JP. 1995. Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproductive output between 1913 to 1991. Colon. Waterbirds. 18(1): 48-59.

Weseloh DVC, Pekarik C, Havelka T, Barrett G, Reid J. 2002. Population trends and colony locations of double-crested cormorants in the Canadian Great Lakes and immediately adjacent areas, 1990-2000: A manager's guide. J. Great Lakes Res. 28(2): 125-144.

Wires LR, Cuthbert FJ. 2009. Characteristics of double-crested cormorant colonies in the U.S. Great Lakes island landscape. J. Great Lakes Res. 36(2): 232-241.

Wires LR. 2015. Migratory bird protection, a crack in the armor: the case of the double-crested cormorant. Avian Conser. Ecol. 10(1). Available from: http://dx.doi.org/10.5751/ACE-00761-100108