

DYNAMIC POPULATIONS, DYNAMIC LANDSCAPES:
CONSERVATION SCIENCE CASE STUDIES OF COLONIAL WATERBIRDS
IN THE NORTH AMERICAN GREAT LAKES

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DEDICATION

To my grandmother, Charlotte Wyman, who was a passionate birder in her later years and who delighted in learning about my avian adventures, and to my undergraduate thesis advisor, Nicholas Rodenhouse, who showed me that I could be a scientist.

ABSTRACT

Colonial animals concentrate locally, presenting different conservation challenges and opportunities than more broadly-distributed species. The Double-crested Cormorant (*Phalacrocorax auritus*) and the Black Tern (*Chlidonias niger*) in the North American Great Lakes provide two contrasting case studies of the challenges and opportunities for conservation and management of colonial waterbirds. I used a combination of historical datasets, new field studies, and statistical modeling to investigate issues surrounding conservation and management of these two birds in Great Lakes. The Double-crested Cormorant, focus of the first case study, has experienced extreme population growth and is now subject to population management at a majority of U.S. Great Lakes colony sites; effects of cormorants and their management on co-nesting waterbird species have remained largely unknown. I observed that nesting among Double-crested Cormorants increased frequency of agonistic interactions for Great Blue Herons (*Ardea herodias*), particularly when nesting on the ground. My research also showed that Black-crowned Night-Heron (*Nycticorax nycticorax*) colony growth was negatively associated with Double-crested Cormorant abundance and implementation of management, while Herring Gull (*Larus argentatus*) and Ring-billed Gull (*Larus delawarensis*) colony growth was positively associated. The Black Tern, subject of the second case study, has been declining for over half a century due to unknown causes, although wetland loss and degradation have likely contributed. I found a positive relationship between increasingly clumped vegetation in Great Lakes coastal wetlands and historical Black Tern colony abandonment. Under current conditions in the region, wetland type and area were critical

parameters in delineating wetlands that were unsuitable for Black Terns from potentially suitable ones. In the ever-changing landscape of the North American Great Lakes, my investigations provide important results to inform future conservation and management actions for these two very different species.

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PREFACE

When you step into a waterbird breeding colony, your senses are immediately assaulted by the cacophony of voices, the myriad social displays, even the stench of tens or hundreds or thousands of animals all living, raising young, and sometimes dying in one place. The visibility and vitality of breeding colonies inspire wonder but also imperil these birds. The concentration of many animals in a single location increases population vulnerability to localized threats, from hunting to land development. Both the Great Auk (*Pinguinus impennis*) and the Passenger Pigeon (*Ectopistes migratorius*) were colonial breeders; they are now classic examples of the human ability to exploit species to extinction. Similarly, the foundation of the American bird conservation movement in the 19th century was motivated by the decline of colonially-breeding terns and herons that were killed so their feathers could adorn women's hats (Kushlan 2012). Yet the concentration of many animals in a single location also presents unique opportunities. Conservation and management can be applied on a small spatial scale while still affecting large numbers of individuals, which is logistically and financially advantageous when resources are limited.

My dissertation research investigated challenges faced by colonial waterbirds in the North American Great Lakes region. The Great Lakes are a globally important area for colonial waterbirds, hosting at least 16 species from three avian orders. Ten of these species are classified as conservation or management priorities, including the two species I focus on in the following pages (Wires *et al.* 2010). Nearly one million individuals

breed annually at hundreds of sites in the Great Lakes proper, while many more breed on inland lakes and rivers in adjacent states and provinces (Cuthbert and Wires 2013).

Despite all the North American Great Lakes have to offer colonial waterbirds, including >32,000 islands and diverse aquatic and terrestrial ecosystems in which to feed and breed (Henson *et al.* 2010), waterbird populations in the Great Lakes face particular challenges from both anthropogenic and natural sources. Great Lakes colonial waterbirds are higher-trophic-level consumers in a contaminated environment; reproduction has suffered in some locations due to eggshell thinning and developmental defects caused by contaminants (Grasman *et al.* 1998). Human development has expanded in the Upper Midwest in recent decades, with most new development occurring along the Great Lakes coastline (Wolter *et al.* 2006). Exotic species from hybrid cattail (*Typha x glauca*) to round goby (*Neogobius melanostomus*) have changed plant and animal communities across the Great Lakes, affecting where colonial waterbirds can live and what they can eat (Mills *et al.* 1993; Tuchman *et al.* 2009; Coleman *et al.* 2012). At the largest scale, Great Lakes water levels fluctuate annually and over the course of years and decades, which results in appearance and disappearance of islands and isthmuses, as well as cycles in coastal vegetation structure (Wilcox and Nichols 2008). Climate change is expected to further alter lake level patterns (Angel and Kunkel 2010).

My dissertation focuses on two case studies of conservation and management challenges faced by two very different species within the Great Lakes colonial waterbird community. Double-crested Cormorants (“cormorants”; *Phalacrocorax auritus*) and Black Terns (*Chlidonias niger*) occupy opposite ends of the spectrum of conservation and

management need. The regional cormorant population has grown dramatically since the 1970s due to federal protection from persecution, banning of organochlorine pesticides, and newly-available prey in the form of non-native fish species (Weseloh *et al.* 1995). To mitigate real or perceived impacts of this population growth, over half of all Great Lakes cormorant colonies are managed, either by oiling eggs to curb reproduction or by culling adults (Wires and Cuthbert 2010). Black Terns, in contrast, have been declining in the Great Lakes region since the mid-twentieth century (Peterjohn and Sauer 1997) and now receive the protection of many state endangered and threatened species lists (Wires *et al.* 2010). Drivers of this decline remain largely unknown, but loss and degradation of wetland breeding habitat is of major concern (Wires *et al.* 2010).

In the first two chapters of my dissertation, I address the question of how cormorant population growth and management affect co-nesters, members of other colonial waterbird species nesting at the same sites. Chapter 1 focuses on cormorants' potential behavioral impacts on individual co-nesters. In Chapter 2, I investigate whether co-nester population growth at colony sites is related to local cormorant abundance and management status. In the second half of my dissertation, I turn my attention to the potential role of habitat availability and quality in the regional decline of the wetland-breeding Black Tern. Chapter 3 uses GLCWS data, historical aerial photographs, and remotely-sensed land use/land-cover data to address the question of how abandonment of colony sites in the Great Lakes relates to landscape changes in and around those sites. Chapter 4 evaluates two variations on a tool to identify and prioritize areas within the Great Lakes region for Black Tern habitat conservation and restoration.

The first chapter of this dissertation was previously published in *Waterbirds* in 2015. The remaining chapters are either in review or in preparation for publication, all in different peer-review journals. These different publication outlets account for any stylistic differences observable across the four chapters.

CHAPTER 1

SPECIES IDENTITY AND NEST LOCATION PREDICT
AGONISTIC INTERACTIONS AT A BREEDING COLONY
OF DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*)
AND GREAT BLUE HERONS (*ARDEA HERODIAS*)

Waterbird colonies provide breeding birds with an important resource: nest sites. Multiple species of colonial waterbirds occupy similar types of nest sites (Burger 1979; Pius and Leberg 1997; Weseloh *et al.* 2002), which can lead to interspecific competition for these sites (Burger 1978; Pius and Leberg 1997), often manifested through agonistic behavior (Brown and Orians 1970). Intense interspecific territoriality may reduce individual reproductive success (Burger 1978; Duckworth 2006). Accordingly, growth of the North American Interior population of Double-crested Cormorants (*Phalacrocorax auritus*; hereafter, “cormorants”) since the 1970s (Weseloh *et al.* 1995; Wires and Cuthbert 2006) has led to concern that cormorants will reduce reproductive success of co-nesting colonial waterbird species through nest-site competition (Weseloh *et al.* 2002). Cormorant management is authorized at some locations in the USA specifically to protect other waterbird species believed to be vulnerable to cormorant presence (U. S. Department of the Interior 2014).

Evidence for negative effects of cormorants on co-nesting waterbirds remains inconclusive. Wading bird abundance has declined at some breeding sites shared with cormorants, but researchers have been unable to identify interspecific competition as the definitive cause of these declines (Skagen *et al.* 2001; Cuthbert *et al.* 2002). Studies of ground-nesting colonies have shown conflicting results on the impacts of cormorants on co-nesters (Somers *et al.* 2007; Somers *et al.* 2011). For example, Herring Gulls (*Larus argentatus*) engaged in more agonistic (combined inter- and intraspecific) interactions when nesting among cormorants (Somers *et al.* 2007), while American White Pelicans (*Pelecanus erythrorhynchos*) engaged in fewer agonistic interactions when nesting

among cormorants (Somers *et al.* 2011), compared to nesting among conspecifics exclusively.

Somers *et al.* (2011) posited that the observed variability of responses to co-nesting with cormorants could be attributable to habitat structure, nest density, or the identity of the species involved. Because cormorants breed both on the ground and in trees (Hatch and Weseloh 1999) and often nest near other species (Cuthbert and Wires 2013), there is considerable variation among colonies in each of these variables. The behavioral literature supports all three hypotheses: habitat structure (Bukacinska and Bukacinski 1993; Jensen *et al.* 2005; Barley and Coleman 2010); nest or territory density (Butler and Trivelpiece 1981; Stokes and Boersma 2000); and/or species identity (Burger 1978; Mott and Maret 2011).

Our study examined the Somers *et al.* (2011) hypotheses that three potential factors (habitat structure, nest density, and species identity) drive the rate of agonistic interactions in a mixed-species breeding colony. At our study site in Meeker County, Minnesota, cormorants and Great Blue Herons (*Ardea herodias*; hereafter, “herons”) nested on the ground and in trees across two islands. Thus, individual cormorants and co-nesters could be observed in a range of nest microenvironments all subject to the same broad environmental conditions.

METHODS

Study Area

Interactions between cormorants and herons were observed at Pigeon Lake, Meeker County, Minnesota (45° 02' 24" N, 94° 20' 53" W). Three islands in this lake have been used for breeding by both species, as well as by American White Pelicans, Great Egrets (*A. alba*) and Black-crowned Night-Herons (*Nycticorax nycticorax*; Wires *et al.* 2006). In 2012, aerial photographs and a ground count of American White Pelican nests provided estimates of nest abundance at the island complex: Great Blue Heron ($n = 159$ nests), Great Egret (8), Double-crested Cormorant (3,309), American White Pelican (191; L. Wires, pers. commun.).

Observations

We observed focal nests of herons and cormorants from 16 April to 11 June 2012. Of the species breeding at the study site, these species were the only two whose nests were both easily visible and abundant. In mid-April, cormorants were completing the nest-building phase of the breeding period and most herons were incubating eggs. Therefore, the colony site was settled before observations began. Focal nests were selected by assigning numbers to all visible nests in each combination of nesting location (tree or ground) and species (heron or cormorant), then randomly selecting 13 nests out of the total available in each category. Selected nests were observed weekly for one 30-min period between 06:55 and 18:15 with a 20–60x spotting telescope from a roadside overlook. One focal nest of ground-nesting herons failed mid-season and the selection

procedure was repeated to choose a replacement from among the ground-nesting heron nests not currently under study. Two focal nests of tree-nesting cormorants failed in the last two weeks of observations and were not replaced, resulting in a total sample size of 53 nests. For each focal nest, nest density was defined on a scale from one to five, corresponding to the number of contiguous territories situated around the nest and/or above it (Butler and Trivelpiece 1981). Values were estimated from aerial and ground photographs of the colony because quarantine of the site following a Newcastle disease outbreak prevented us from measuring nest density directly.

Agonistic behaviors (Table 1) were identified according to published ethograms for each species (van Tets 1965; Mock 1976). Both interspecific and intraspecific agonistic interactions were recorded, along with species identities of the birds involved. Potential effects of time of day on interaction rate were minimized by alternating species and nest locations throughout the day (e.g., a ground-nesting heron observation would be followed by a tree-nesting cormorant, then a tree-nesting heron, then a ground-nesting cormorant) and by observing nests in the same order from week to week. Individuals were not marked and could not be reliably distinguished on the basis of plumage or size, so the smallest unit of study was the nest. When both members of a nesting pair were present at the nest, only the incubating or brooding bird's interactions were recorded to promote consistency with nests where only one adult was present.

Statistical Analyses

Generalized linear mixed models were constructed representing the study's alternative hypotheses (i.e., species identity, nest density, and/or nest location influence frequency of agonistic interactions; Table 2). Two response variables were considered: 1) total number of agonistic interactions (both interspecific and intraspecific) involving the focal nest within a 30-min observation period; and 2) number of interspecific agonistic interactions involving the focal nest within a 30-min observation period. Each model contained covariates controlling for date of observation, time of day of observation, and proportion of the four nearest neighboring nests occupied by heterospecific individuals. All these factors may influence rates of aggression (Burger 1984; Bukacinska and Bukacinski 1994; Pius and Leberg 1997; Somers *et al.* 2011). Models of total count of inter- and intraspecific interactions including species as a covariate also included an interaction term for species and proportion of heterospecific neighbors. A random intercept term accounted for non-independence of observations made on the same nest (Zuur *et al.* 2009).

Model fitting and selection were performed in program R (R Development Core Team 2012) using the 'glmmADMB' package (Fournier *et al.* 2012; Skaug *et al.* 2014). The first step of model selection determined appropriate error structure for the full model, considering four types of regression models: Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial. Negative binomial models provided the best fit to the full model for both response variables and were used for selection among reduced models representing alternative hypotheses (Table 2). Model selection was

accomplished using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). In tables, we only report models with a difference of $AIC \leq 12$ compared to the top model.

RESULTS

During 412, 30-min observation periods, we observed 436 agonistic interactions between nesting individuals at Pigeon Lake. Interspecific interactions between cormorants and herons occurred in 54 observation periods (13.1% of all periods). Intraspecific interactions occurred in six (2.9%) heron observation periods and in 104 (50.7%) cormorant observation periods. Most interactions of either type occurred between the focal nest and occupants of neighboring nests. No interactions occurred in 60% of observation periods.

Species identity and nest location were more important predictors of total number of agonistic interactions (interspecific and intraspecific combined) than nest density (Table 3). Great Blue Herons engaged in fewer total interactions than Double-crested Cormorants in the same location, while tree-nesting birds engaged in fewer total interactions than ground-nesting birds (Fig. 1). Proportion of heterospecific neighbors also influenced total number of agonistic interactions: herons nesting among conspecifics had fewer total interactions than herons nesting among cormorants, while cormorants nesting among conspecifics had more total interactions than cormorants nesting among herons (Fig. 1).

Nest location was a more important predictor of interspecific interaction rate than species identity or nest density (Table 4). Tree-nesting birds engaged in fewer

interspecific interactions than ground-nesters. Heterospecific neighbors also had a strong positive effect on number of interspecific agonistic interactions (Fig. 2).

DISCUSSION

Our observations at the Pigeon Lake waterbird colony support the hypotheses proposed by Somers *et al.* (2011) that species identity and habitat structure are related to the rate of agonistic interactions among nesting individuals. Species identity of neighbors also had a strong influence on agonistic behavior; arrangement of nests within a colony matters as much as overall species composition.

These results, along with previous research (Skagen *et al.* 2001; Cuthbert *et al.* 2002; Somers *et al.* 2007; Somers *et al.* 2011), suggest that some co-nesting species may be more affected by nesting among cormorants than others. Spatial structuring of nests within a colony is important; interaction rates can vary with nest location and species identity of neighbors. According to our study, rates of agonistic interaction will likely be highest among ground-nesters. Birds that interact little with conspecific neighbors in single-species colonies will likely engage in more total interactions in mixed-species colonies because of added interspecific interactions. At Pigeon Lake, heron interactions with conspecific neighbors were limited, so presence of cormorant neighbors increased the total number of interactions involving herons. Future research on interactions between cormorants and co-nesters should determine whether, and to what degree, co-nester reproductive success declines when co-nesters engage in agonistic interactions with cormorants.

As cormorant population management has been implemented in the USA over the past two decades, cormorant interactions with other members of the ecological community have transitioned from a scientific to a political issue. Although this study suggests that Great Blue Heron behavior changes in the presence of co-nesting Double-crested Cormorants, it does not provide evidence either to support or discourage management activities. Other issues (e.g., reproductive impacts, potential impacts of control activities) must also be considered in decisions of whether and how to apply management to cormorant populations.

CHAPTER 2

GREAT LAKES DOUBLE-CRESTED CORMORANT MANAGEMENT
AFFECTS CO-NESTER COLONY GROWTH

The population of Double-crested Cormorants (*Phalacrocorax auritus*; hereafter, “DCCO”) in the North American Great Lakes has grown dramatically since the mid-twentieth century, largely due to protection from persecution and bans on organochlorine pesticides (Weseloh *et al.* 1995). Across the 5 Great Lakes and their connecting waterways, U.S. and Canadian surveys observed only 598 nesting pairs of DCCO in 1977; in 2007, 97,188 nesting pairs were recorded (Wyman *et al.* 2016). DCCO population growth was initially seen as a conservation success story, but as growth continued, attitudes towards DCCO changed in the region (Muter *et al.* 2009). Concerns arose over real or perceived effects of these piscivorous birds on fisheries, of their guano on nest-site vegetation, and of their presence and behavior on other colonially-breeding waterbirds that share breeding sites with DCCO (Weseloh *et al.* 2002).

In 2003, the U.S. Fish and Wildlife Service established a Public Resource Depredation Order (50 CFR 21.48), enabling DCCO colonies in U.S. Great Lakes states to be managed to reduce colony sizes. By 2007, a majority of DCCO colony sites in the U.S. Great Lakes had been subject to some form of management (Wires and Cuthbert 2010). Management at Canadian Great Lakes DCCO colonies first occurred in 2004, but was limited to only a few sites (Wires 2014). The 2 primary methods of management used are spraying eggs with food-grade corn oil so that embryos asphyxiate, and culling adult birds at breeding colonies during the nesting season (Blokpoel and Hamilton 1989; Wires 2014). Less frequently, birds are culled or harassed outside the breeding season or nests are destroyed (Dorr *et al.* 2012; Farquhar *et al.* 2012).

DCCO rarely nest alone in the Great Lakes (Wires and Cuthbert 2010; Wyman *et al.* 2016), so DCCO abundance and DCCO management have become relevant concerns for conservation and management of co-nesting waterbird species. Declines in wading bird abundance have been observed at some shared breeding sites, but authors of these studies were unable to conclusively link declines directly or indirectly to activities of DCCO (Skagen *et al.* 2001; Cuthbert *et al.* 2002). On the other hand, DCCO presence has been observed to change the frequency with which co-nesters engage in agonistic interactions, particularly in ground-nesting colonies (Somers *et al.* 2007; Somers *et al.* 2011; Wyman and Cuthbert 2015). In one case, DCCO were associated with reduced Herring Gull (*Larus argentatus*) breeding success, although human disturbance was a confounding factor in the study (Somers *et al.* 2007). Co-nester responses to DCCO management have received little direct research attention. However, DCCO have been reported to exhibit increased interspecific aggression as a result of human disturbance (Drapeau *et al.* 1984), important because most management operations require humans to enter the breeding colony (T.J. Doyle, U.S. Fish and Wildlife Service, personal communication). Despite the useful insights provided by these studies, they focus on the individual as the experimental unit and do not provide information about how effects scale up to the level of the colony or population. Identifying potential large-scale impacts of both DCCO and their management is crucial for designing responsible DCCO management plans.

The goal of our study was to quantify potential impacts of DCCO abundance and management on changes in colony size of co-nesting colonial waterbirds. We focused on

4 species that are the most common co-nesters of DCCO in the North American Great Lakes: Great Blue Heron (*Ardea herodias*), Black-crowned Night-Heron (*Nycticorax nycticorax*), Ring-billed Gull (*Larus delawarensis*), and Herring Gull (Wires and Cuthbert 2010). For each of these species we examined 4 hypotheses: (1) co-nester colony growth is related to DCCO abundance; (2) co-nester colony growth is related to the presence or absence of DCCO management; (3) co-nester colony growth is related to the intensity of DCCO management; and (4) impacts of DCCO management differ according to the type of management (nest oiling or culling) used.

STUDY AREA

Our study relied on waterbird colony surveys conducted between 1976 and 2010 and therefore on the study areas of those surveys. The study area of the Great Lakes Colonial Waterbird Survey ("GLCWS", Scharf 1978; Scharf and Shugart 1998; Scharf 1998; Cuthbert *et al.* 2010; Cuthbert and Wires 2013), from which U.S. waterbird colony data were drawn, included U.S. waters of the 5 Great Lakes (Ontario, Erie, Huron, Michigan, and Superior) as well as their connecting waterways (St. Lawrence River, Niagara River, Detroit River and Lake St. Clair, and St. Marys River). Between Massena, NY, and Pigeon Point, MN, the U.S. coastline up to 1 km inland was also included in the study area. The eastern boundary of the study area was extended to Massena, NY, in the second GLCWS (1989-1991); the first GLCWS did not include the St. Lawrence River (Cuthbert *et al.* 2010).

The study area for Canadian surveys included Canadian waters of 4 of the Great Lakes (Ontario, Erie, Huron, and Superior), as well as Canadian waters of the St. Lawrence River, Niagara River, and Detroit River. Colonies located along the mainland coastline between Cornwall, ON, and the U.S.-Canadian border at the west end of Lake Superior were also included (Morris *et al.* 2003).

METHODS

Waterbird Colony Data

The GLCWS in the U.S. (Scharf 1978; Scharf 1998; Scharf and Shugart 1998; Cuthbert *et al.* 2010; Cuthbert and Wires 2013) and similar surveys in Canada (D.J. Moore, Canadian Wildlife Service, personal communication) provided all data on waterbird colony locations and nest abundances for this study. Cuthbert and Wires (2013) describe the methods used in these surveys to locate active waterbird colonies and to census nesting individuals of all colonial waterbird species at each active colony. Four surveys were conducted in the U.S. and Canada during the years 1976-2010, with the first survey in 1976-1980, the second in 1989-1991, the third in 1997-2000, and the fourth in 2007-2010 (Morris *et al.* 2003; Cuthbert and Wires 2013).

In the remainder of the “Methods” and “Results” sections, we use the term “colony” to describe a group of individuals of a single species nesting at a site, rather than all individuals nesting at the site. Similarly, nest abundance implies abundance of a single species rather than the combined abundance of all species nesting at a site.

Response Variable

Our response variable for all models was a colony growth index. Because sites may be abandoned or newly colonized between surveys, the index value in survey s was defined, following Guillaumet and colleagues (2014), as:

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

where N_s and N_{s-1} represent nest abundance in survey s and survey $s - 1$, respectively.

Using this definition, the colony growth index takes values from -1 to 1, where -1 indicates colony abandonment and 1 indicates colonization. Values between -1 and 0 indicate declining nest abundance, while values between 0 and 1 indicate increasing nest abundance. Sites that were unoccupied from one survey to the next were assigned an index value of 0 to indicate no change. Guillaumet and colleagues (2014) referred to this calculation as “growth rate”; we prefer “growth index” here because we measured colony growth over time periods that varied slightly in length according to when surveys were completed.

Model Covariates

Many variables, both intrinsic and extrinsic to the colony itself, may influence the occupancy and abundance dynamics of colonial waterbirds. We were primarily interested in covariates related to DCCO abundance and DCCO management. Data for the former covariate were obtained from the GLCWS and Canadian surveys (Cuthbert and Wires 2013, D.J. Moore, personal communication). Data on DCCO management in the U.S. were obtained from the U.S. Fish and Wildlife Service and included information on

locations, dates, numbers of DCCO eggs oiled, numbers of nests destroyed, and numbers of DCCO culled from the beginning of legal management in the Great Lakes in 1999 through 2010 (T.J. Doyle, personal communication). Because nest destruction was a relatively rare management strategy in these data, for our analysis we grouped nest destruction with egg oiling as a contrasting management strategy to culling. Management of DCCO in Canada has been rare and sometimes is restricted to tactics that simply discourage nesting (Wires 2014). Managed sites in Canada were identified by Wires (2014); we also referred to relevant government reports as needed to obtain numerical data. We focused on 3 variables and 3 time periods in our models: number of management-related visits, number of nests oiled/destroyed, and number of DCCO culled in the year of survey and the 2 previous breeding seasons.

We controlled for the influence of 5 additional variables in modeling the relationship between colony growth index and DCCO abundance and management. Wyman and colleagues (2014) previously identified historical nest abundance, historical species richness, and flood potential of a colony site as significant influences on occupancy dynamics of Great Lakes colonial waterbirds. The GLCWS and Canadian surveys (Cuthbert and Wires 2013, D.J. Moore, personal communication) provided estimates of abundance and species richness by colony site for the survey previous to the one for which the response variable, colony growth index, was calculated. Values for flood potential were drawn primarily from GLCWS data, with expert opinion filling in gaps in GLCWS observers' records. A site was considered as having potential to flood if nest elevation was <2 m above water level, if flooding was noted as a potential threat to

nesting, or if the site was actually flooded during a survey. Flood potential was determined for the site as a whole rather than for a particular species or survey period (Wyman *et al.* 2014).

To avoid falsely attributing persistent trends in colony growth index to DCCO or their management as both became more widespread in later surveys, we included colony growth index of the colony in the previous inter-survey period as a predictor of colony growth index in the period of interest. The colony growth index was calculated as described above for the response variable.

Because one of the ways in which DCCO management might affect co-nesters is through disturbance at the colony site, we sought to control for other sources of colony site disturbance. We created a dummy variable with value “0” for no known disturbances since the previous survey and “1” for disturbances known or suspected since the previous survey, considering illegal DCCO management activities (e.g., culling without a permit, release of predators into colonies), disturbance caused by human recreation, and researcher disturbance. Lacking good records on the former 2 sources, we relied on our own knowledge of illegal management and recreational disturbance at sites. Some Great Lakes waterbird colonies have a long history of researcher disturbance, so we used a literature search to identify sites in the Great Lakes where research occurred during each of the survey periods. We searched Web of Science (Thomson Reuters, New York, USA) for publications published between 1976 and the present including “Great Lakes” as a topic and the terms “gull”, “heron”, “cormorant”, “pelican”, “tern”, “egret”, “(colon* and *bird)”, or “(colon* and bird)” in the title. This search identified 327 publications

describing researcher disturbance at colony sites within the Great Lakes; locations named in these publications were coded as experiencing known disturbance within the time period indicated by the publication. We did not count research conducted on birds salvaged from management operations as separate researcher disturbance.

Statistical Analyses

We used linear mixed-effects models to relate DCCO abundance and management, along with nuisance covariates, to co-nester colony growth index values. For each species, we fit 4 models (see Appendix for full model specifications in statistical notation). All models included historical nest abundance, historical species richness, flood potential, historical growth index, other disturbance, and DCCO abundance as fixed effects, and survey period, water body, and site as random effects. For herring gulls, we excluded the random effect of site because it interfered with model convergence and site-level effects were expected to even out given ~1500 unique herring gull colony sites.

To determine the effect of DCCO management presence on co-nester colony growth index, we added a covariate indicating whether DCCO management had been applied at the colony site since the preceding survey. To determine the effect of increasing management intensity in the form of number of management-related visits to the site, we added covariates for number of management-related site visits in the survey year and the preceding 2 years, in addition to presence/absence of management. To determine the effect of increasing management intensity in the form of number of DCCO affected, we included covariates for number of nests oiled and number of DCCO culled

in the survey year and the preceding 2 years. If management in the survey year occurred after the colony census, management covariates for that year equaled zero. Prior to model fitting, all numerical covariates were scaled to have a standard deviation of 1.

We fit the models using a Bayesian approach to enable modeling of missing data. Percentages of missing data for each covariate ranged from 0% (other disturbance, most management variables) to 33% (prior colony growth index). Distributions for missing data were constructed using means and standard deviations of observed data for the species in question. Mimicking empirical distributions as much as possible, historical species richness, number of management visits, number of nests oiled, and number of adults culled were modeled with normal distributions truncated at 0; historical abundance and DCCO abundance were modeled with exponential distributions; flood potential was modeled with a Bernoulli distribution; and prior colony growth index was modeled with a uniform distribution. For parameters, we used diffuse normal priors for effects of linear predictors and diffuse uniform priors for variance parameters.

Using Markov chain Monte Carlo simulation implemented in JAGS (version 4.1.0, sourceforge.net/projects/mcmc-jags/files, accessed 12 Feb 2016) and the package 'R2jags' (version 0.5-7, cran.r-project.org/web/packages/R2jags/index.html, accessed 25 Jan 2016) in program R (version 3.2.3, www.r-project.org, accessed 25 Jan 2016), we ran 3 simultaneous chains for 30,000 – 50,000 iterations, as determined by the number of iterations required to achieve (1) Monte Carlo standard error <2% of posterior distribution standard deviation and (2) R-hat statistics (Gelman and Rubin 1992) of <1.1 for all parameters. In addition to R-hat, we monitored convergence by visual inspection

of trace plots. A burn-in period of 2000 iterations was discarded and chains were thinned by 10 due to computational memory limitations.

We evaluated model fit using Bayesian p-values (King *et al.* 2010), where the discrepancy function was the sum of squared residuals. A p-value of 0.5 indicates good model fit, specifically, that the fit of the model to the observed data is no better or worse than the fit of the model to data simulated from the model itself. Bayesian p-values range in value from 0 to 1 (King *et al.* 2010).

RESULTS

DCCO colonies have been well distributed across the North American Great Lakes, as have DCCO management activities in U.S. waters (Fig. 3). Four common co-nesters of DCCO shared colony sites with DCCO in 12-43% of occurrences in the North American Great Lakes between 1976 and 2010 (Table 5). Between 1% and 7% of co-nesting occurrences also occurred in the presence of DCCO management (Table 5). When considering the fourth survey period alone, 4%-16% of co-nesters' colony sites were subject to DCCO management.

DCCO abundance was associated with co-nester colony growth index for all species except Great Blue Herons, but the direction of association varied (Fig. 4). DCCO abundance was associated with a lower or more negative colony growth index for Black-crowned Night-Herons, while DCCO abundance was associated with a higher colony growth index for the 2 gull species. These effects remained almost identical in size and

magnitude regardless of which management variables were added to the model (Tables S1-S16, available in Appendix).

The presence of management was associated with a strongly increased colony growth index for Herring Gulls (Fig. 4). A positive effect was also suggested for Ring-billed Gulls, with most of the posterior density located above 0. For Black-crowned Night-Herons, the presence of management had a negative effect on colony growth index (Fig. 4). As with DCCO abundance, Great Blue Heron colony growth index values were not notably responsive to the presence of DCCO management (Fig. 4).

We measured management intensity in 2 ways: how many visits were made to perform management activities, and how many DCCO were affected by management in terms of nests oiled and adults culled. In the year prior to survey, more visits were weakly associated with a reduced colony growth index for all species (Fig. 5; Tables S3, S7, S11, and S15). For Black-crowned Night-Herons, this association was true for the current year and 2 years previously as well (Fig. 5; Table S7). The approximate linearity of the relationship between number of visits and colony growth index for Black-crowned Night-Herons showed that the effect of the presence of management alone disappears when management effort is taken into account (Fig. 5, Table S7). For all other species, the presence of management still had an effect beyond the number of visits, as presence of management changed the slope of the relationship between number of visits and colony growth index for visit numbers >0 (Fig. 5).

Effects on co-nesters often differed according to the management method used (Fig. 5; Tables S4, S8, S12, and S16). Despite the strong positive effect of presence of

management on Herring Gull colony growth index, index values had no association with number of DCCO culled, and mixed responses to number of nests oiled depending on the lag time between management and survey (Fig. 5, Table S16). Response of Black-crowned Night-Heron colony growth index to egg-oiling in the year prior to survey was predominantly negative with 95% credible intervals that did not overlap 0 (Table S8), but responses were less consistently negative for this species for other lag times of nest oiling and for culling. According to posterior distribution means, Great Blue Herons showed increased colony growth index associated with both culling and nest oiling in the survey year (Fig. 5). However, the relationship between Great Blue Heron colony growth index and nest oiling in the survey year also had considerable posterior density to suggest a negative response (Table S4).

Models of co-nester colony growth indices fit excellently, with Bayesian p-values within the range 0.49-0.52. Growth indices of all species were negatively related to prior colony growth index value and historical nest abundance, which were included in our models to control for influences other than DCCO and their management.

DISCUSSION

Four colonial waterbird species that commonly co-nest with DCCO in the Great Lakes showed variable responses to DCCO presence and management (Figs. 4, 5). These results suggest that the prevailing opinion that DCCO management can only be neutral or beneficial to co-nesting waterbird populations (U.S. Fish and Wildlife Service 2014) is an oversimplification. Excellent model fit and consistency of model results with other

expected population processes like density-dependent growth give strength to these findings.

Gull Response to DCCO Abundance and Management

Both Herring Gulls and Ring-billed Gulls showed a strongly positive response to DCCO abundance, contrary to Somers and colleagues' earlier finding of reduced reproductive success in Herring Gulls nesting with DCCO (Somers *et al.* 2007). Somers and colleagues' Herring Gull work may have been confounded by human disturbance (Somers *et al.* 2007; Somers *et al.* 2011), but according to our fitted models, Herring Gulls in particular have an almost exclusively positive response to presence of DCCO management as well, a situation in which human disturbance is almost unavoidable. Indeed, there are indications that DCCO management is associated with increased Herring Gull nest success (B.S. Dorr, USDA Wildlife Services, personal communication). Several researchers have shown that gulls can take advantage of human disturbance of cormorant colonies to depredate cormorant nests (Kury and Gochfeld 1975; Ellison and Cleary 1978; DesGranges and Reed 1981), and this food resource may explain the boost in colony growth index. Gull depredation following researcher or management disturbance has been observed to affect as much as 95-100% of DCCO nests, depending on gull colony size and location, where DCCO were nesting, and timing of disturbance, among other factors (F.J.C., personal observation; N.E. Seefelt, Central Michigan University, personal communication). Gull depredation of DCCO nests during management has actually caused some agencies to shift to nighttime management (Duerr

et al. 2007). If part of the benefit of nest oiling is to keep birds sitting on inviable eggs for an extended period of time to minimize the probability of re-nesting (Blokpoel and Hamilton 1989), gull depredation during the course of management can counteract that goal.

Despite a large positive effect of the presence of management on colony growth index for Herring Gulls in particular, the species did not show a strong positive response with increasing intensity of management (Fig. 5). The lack of response to culling in Herring Gull colony growth index is logical to some extent; culling is often applied to tree-nesting colonies (McGregor and Davis 2012), while Herring Gulls are typically ground-nesters and ground-foragers (Pierotti and Good 1994). Herring Gulls did show a positive response to egg-oiling in one year (Fig. 5), as might be expected because oiling more nests may indicate a longer disturbance to the colony site and therefore more opportunities for depredation. That these effects were not more consistent or stronger suggests that any disturbance for management purposes is advantageous for gulls, but that the marginal benefit for the gull colony of depredating a DCCO nest may decline as more nests are available for depredation.

Black-crowned Night-Heron Response to DCCO Abundance and Management

Both DCCO presence and DCCO management reduced Black-crowned Night-Heron colony growth index, with more management visits associated with greater reductions (Figs. 4, 5). Cuthbert and colleagues (2002) similarly reported an association between Black-crowned Night-Heron declines at colony sites and DCCO presence but

observed no direct interactions between Black-crowned Night-Herons and DCCO at 2 colony sites in northern Lake Michigan, nor did they find any overlap in the individual trees that the species were using for nesting. The impact of DCCO on nest site vegetation is a potential alternative mechanism for DCCO abundance to affect black-crowned night-heron colony growth index. Higher DCCO nest density is associated with greater nutrient inputs to the soil underneath nests (Rush *et al.* 2011), and with Gray Herons (*Ardea cinerea*), higher nest density and increased nutrient input have been linked with reduced understory vegetation (Ueno *et al.* 2006).

Black-crowned Night-Herons are considered of moderate conservation concern at the continental scale and a conservation priority species within the Upper Mississippi River-Great Lakes region (Wires *et al.* 2010). Alleviation of DCCO impacts to Black-crowned Night-Herons has been invoked as a reason for DCCO management and a dataset on DCCO management impacts on Black-crowned Night-Herons in eastern Lake Ontario previously suggested a positive effect of management (Farquhar *et al.* 2012). Other local datasets lack clear trends for Black-crowned Night-Herons in relation to DCCO management (Wires *et al.* 2011; Thorndyke and Dobbie 2013). Our results show that while occasional positive responses to DCCO management may occur, negative responses are likely to be much more common (Fig. 4). In our fitted models, the negative relationship between number of management visits in any year and Black-crowned Night-Heron colony growth index contrasted with inconsistent responses to the number of DCCO affected by management. This contrast suggests that disturbance may be the most problematic part of DCCO management for Black-crowned Night-Herons, and it is

a species that can be sensitive to human disturbance (Tremblay and Ellison 1979; Wires *et al.* 2010).

Great Blue Heron Response to DCCO Abundance and Management

According to our fitted models, Great Blue Herons did not appear to be substantially affected by DCCO abundance nor by the presence of DCCO management at the colony site (Fig. 4). At the level of the individual, DCCO presence is associated with behavioral changes in nesting Great Blue Herons; Great Blue Herons engage in more agonistic interactions when nesting near DCCO (Wyman and Cuthbert 2015) and may abandon nests (Skagen *et al.* 2001). The lack of relationship between DCCO abundance and Great Blue Heron colony growth index suggests that these individual effects of DCCO on Great Blue Herons do not translate directly to the colony level as a whole.

Great Blue Heron mean responses to management activity were quite variable (Fig. 5), but the only management intensity variable for which the posterior distribution's 95% credible interval did not overlap 0 was culling in the year of survey (Table S4). Culling is the predominant management approach for tree-nesting DCCO colonies. Removal of tree-nesting DCCO may open up space at the colony site for late-arriving or re-nesting Great Blue Herons, which would increase Great Blue Heron colony size. However, the neutral to negative effects of culling on colony growth index in the 2 years prior to survey suggests that possible benefits of culling for Great Blue Herons are only temporary.

Methodological Limitations

The definition we used for colony growth index, in which the index ranged from -1 to 1 and incorporated site colonization and colony extinction, had important benefits for modeling. Many colonies in the Great Lakes change occupancy status over a decadal timeframe (Cuthbert and Wires 2013), and limiting our models to only those colonies that were continuously occupied as required by traditional definitions of growth rate would have greatly reduced sample size for our analysis. Further, by incorporating all colony occupancy and growth patterns into a single response variable, the model remained relatively simple and allowed us to estimate parameters with good precision. The extremely good fit of our models to the data indicates the adequacy of our method.

Nevertheless, our colony growth index has weaknesses in its ability to represent some biological processes. For example, colonization of a site is always defined as an index value of 1 regardless of the number of colonists, so a colony that experienced growth from 10 individuals to 1000 would have a lower index value than a newly established colony of 5 individuals. A similar issue exists for extinction of a colony relative to dramatic size decline of persistent colonies. On the one hand, a case could be made that colonization and extinction are extremes of colony growth and decline, as they are represented in the colony growth index. On the other hand, they are in some ways fundamentally different processes. The ideal solution would be development of models that marry abundance and occupancy dynamics submodels. We attempted such a model but encountered difficulties with our count data, which did not follow a Poisson or zero-inflated Poisson distribution, and the properties of continuous as compared to discrete

distributions proved problematic in developing an abundance submodel that allowed for colony extinction when we took colony growth index as the response variable.

MANAGEMENT IMPLICATIONS

A responsible management strategy for DCCO needs to take into account the co-nesting species that may be affected by management activities, including how those species typically respond to DCCO management and what conservation or management concerns exist for the co-nesting species themselves. Herring and Ring-billed Gulls are of low conservation concern given their abundance and overall population stability in the Great Lakes region (Wires *et al.* 2010; Cuthbert and Wires 2013). However, in several areas they are seen as pests and as requiring population management themselves (Pierotti and Good 1994; Wires *et al.* 2010; Morris *et al.* 2011). In these situations, if DCCO management is deemed desirable, management at shared colony sites may best be conducted at night, when gulls are unlikely to depredate unattended DCCO nests (Duerr *et al.* 2007) and benefit from DCCO management.

Great Blue Herons are not of conservation concern regionally (Wires *et al.* 2010), and our models suggest that they are relatively insensitive to the presence of either DCCO or their management. Where DCCO management is desired at colony sites shared with great blue herons, no special considerations are suggested by the results of our study apart from a general respect for minimizing disturbance to the co-nesters. In contrast, Black-crowned Night-Herons have declined in the Great Lakes since the 1970s (Rush *et al.* 2015) and, according to our fitted models, respond negatively to both increasing

DCCO abundance and to increasing numbers of visits for DCCO management purposes. However, there are local exceptions where DCCO management has resulted in increased Black-crowned Night-Heron abundance (Farquhar *et al.* 2012). Managers should carefully consider whether DCCO management is truly necessary near nesting Black-crowned Night-Herons, and if management is implemented, conscientious monitoring is imperative to determine how the Black-crowned Night-Herons respond. Because Black-crowned Night-Herons often nest in understory vegetation rather than in the tree canopy or on the ground like DCCO (Hothem *et al.* 2010), and because habitat loss continues to be a significant threat to Black-crowned Night-Herons (Wires *et al.* 2010), conservation activities for Black-crowned Night-Herons may prefer to focus on protecting or restoring habitat away from where DCCO nest abundantly. Such a strategy would help minimize conflict between the 2 species and reduce use of DCCO management at Black-crowned Night-Heron colony sites.

CHAPTER 3

BLACK TERN (*CHLIDONIAS NIGER*) BREEDING SITE ABANDONMENT IN
U.S. GREAT LAKES COASTAL WETLANDS IS PREDICTED BY
HISTORICAL ABUNDANCE AND PATTERNS OF EMERGENT VEGETATION

Despite important recent advances in knowledge of Black Tern (*Chlidonias niger*) biology (e.g., Shealer *et al.* 2014; Shealer 2014; van der Winden *et al.* 2014), many questions remain about the population dynamics of this colonially-breeding waterbird. The species nests in groups of typically two to 50 breeding pairs in deep-water wetlands, where they place their nests on floating substrates that are difficult for both predators and scientists to access (Shuford 1999). Among the most pressing unanswered questions about North American Black Tern populations are the reasons for the Black Tern's steady decline in North America since the mid-twentieth century, particularly in the eastern part of the continent (Peterjohn and Sauer 1997). In the Great Lakes region, Matteson and colleagues report an almost 70% decline in Black Terns in Wisconsin between 1980 and 2011 (Matteson *et al.* 2012) and the binational Great Lakes Marsh Monitoring Program estimates an average decline of 4.9% per year between 1996 and 2013 in the southern Great Lakes basin (Tozer 2016). In coastal wetlands along the shoreline of the U.S. Great Lakes, the number of terns declined by 42% and the number of colonies by 58% between 1999 and 2009 (Cuthbert and Wires 2013). Although Black Terns remain abundant in the Prairie Pothole Region of central North America at present, they are predicted to lose 97% of suitable nesting sites there by 2100 due to climate change (Steen and Powell 2012).

Despite some notable exceptions (Nisbet 1997; D. Shealer, pers. comm.), many scientists view continuing wetland habitat loss and degradation as the major barrier to Black Tern conservation in North America (Heath *et al.* 2009). Both the Great Lakes Colonial Waterbird Survey (Cuthbert and Wires 2013) and the Wisconsin Black Tern

Survey (Matteson *et al.* 2012) have documented greater declines in number of colony sites than in population size in their respective survey regions, suggesting that availability of suitable breeding habitat is limited. Indeed, previous research has reported specific habitat preferences for Black Terns in terms of wetland vegetation structure and composition (Hickey and Malecki 1997; Maxson *et al.* 2007). Invasive emergent plants have been changing characteristics of Great Lakes wetland vegetation over the past several decades, most notably a European genotype of common reed (*Phragmites australis*), hybrid cattail (*Typha x glauca*), and reed canary grass (*Phalaris arundinacea*), each of which can form dense, monotypic stands (Trebitz and Taylor 2007; Tuchman *et al.* 2009; Mitchell *et al.* 2011). Concentration of Black Terns at a limited number of breeding sites is concerning because it increases population vulnerability to natural disasters or other site-based stochastic events which could further their decline.

Managing for the Black Tern's success across its range has become imperative considering current declines and expected future habitat loss due to climate change (Steen and Powell 2012). The long history of colonial waterbird monitoring and management in the Great Lakes (Ludwig 1962; Morris *et al.* 1992; Cuthbert and Wires 2013) and current regional interest in Black Terns (Soulliere *et al.* 2007; Wires *et al.* 2010) make this region an apt focus for conservation efforts. Our study takes a unique regional and historical perspective to identify important predictors of Black Tern colony abandonment in U.S. Great Lakes coastal wetlands. We investigated 14 local and landscape-scale variables for their ability to predict colony abandonment over the approximately decadal period between organized surveys conducted between 1976 and 2009. This multiscale approach

reflects repeated findings in prairie ecosystems that Black Tern colony site use is responsive to landscape features beyond the immediate habitat (Brown and Dinsmore 1986; Naugle *et al.* 1999a; Naugle *et al.* 1999b; Naugle *et al.* 2000). Identification of key local habitat and landscape features influencing Black Tern colony persistence can allow development of conservation and management strategies that target these features to reduce probability of future colony abandonment.

METHODS

Study Area

The study area for this research included the U.S. coastline of the five North American Great Lakes and their connecting waterways from Pigeon Point, Minnesota, to Massena, New York. This study area aligned with that of the Great Lakes Colonial Waterbird Survey, which supplied data on historical Black Tern colonies (see “Colony occupancy data”). Within the study area, Black Terns breed in coastal emergent wetlands that range in type from open or protected embayments to river deltas to channelside wetlands (Albert 2003). Sources of disturbance to these wetlands in the latter half of the twentieth century and the beginning of the twenty-first century included natural disturbances like fluctuating lake levels (Albert 2003; Gronewold *et al.* 2013) as well as anthropogenic disturbances like invasion by exotic plants (Trebitz and Taylor 2007; Tulbure *et al.* 2007; Tulbure and Johnston 2010) and changes in adjacent land use (Wolter *et al.* 2006). These disturbances have been shown to alter the structure and composition of communities of plants, diatoms, macroinvertebrates, amphibians, fishes,

and birds living in the marshes (Brazner 1997; Albert 2003; Brazner *et al.* 2007; Trebitz *et al.* 2009).

Colony Occupancy Data

The dataset included 101 observations of Black Tern colony abandonment or persistence at 78 colony sites on the U.S. Great Lakes (Fig. 6), drawn from the U.S. database of the Great Lakes Colonial Waterbird Survey (Cuthbert and Wires 2013). The Great Lakes Colonial Waterbird Survey recorded locations of active Black Tern colonies and estimated nest abundance at these sites through surveys in 1976-1977 (Scharf 1978), 1990-1991 (Scharf and Shugart 1998), 1998-1999 (Cuthbert *et al.* 2010), and 2008-2009 (Cuthbert and Wires 2013). Eight sites where the Great Lakes Colonial Waterbird Survey had recorded Black Tern nesting were excluded from the dataset due to missing location data. Black Terns were not a main focus of the 1976-1977 survey and colonies were located incidental to colonies of other colonial waterbird species (W. Scharf, personal communication); search effort has been more thorough throughout the study area in more recent surveys. For the present study, the observation period for determining colony abandonment was the approximately decadal period between detection of an active colony at a site and the subsequent survey. Fifty-six sites were occupied only once within the first three survey periods, providing one observation for each of these sites. Two observations were available for 21 sites, and three observations were available for one site. Because of the inaccessibility of most Black Tern nest locations, the majority of nest estimates were obtained by counting the number of birds that flushed when a boat or

wading investigator entered the colony area rather than a complete visual census of nests (Cuthbert and Wires 2013).

Covariate Data

We considered 14 potential predictors of colony site abandonment (Table 6), most of which measured changes in the landscape in and around a site during the observation period and quality of the landscape at the end of the observation period. We defined a “site” as all open water and herbaceous wetland within a circle with 600-m radius centered at the recorded point location of Black Tern nesting. The 600-m radius was based on the maximum recorded distance between Black Tern nests within a colony (Heath *et al.* 2009). All spatial analyses were performed using ArcGIS version 10.2 (Esri, Redlands, CA).

Within the area of the colony site, we measured four covariates to characterize vegetation. We used historical aerial photographs from the U.S. Department of Agriculture Farm Service Agency’s Aerial Photography Field Office (Salt Lake City, UT) to digitize all emergent vegetation at the site for each survey period. Image sources included the Farm Service Agency (1974-1990; 1:40,000 scale; black and white), National Aerial Photography Program (1992-1999; 1:40,000 scale; black and white or color infrared), National High Altitude Program (1981; 1:60,000 scale; color infrared), National Resource Conservation Service (1976-1979; 1:38,000-1:48,000 scale; black and white), and National Agricultural Imagery Program (2004-2009; 1-meter pixel resolution; natural color). Photographs from all sources except the National Agricultural Imagery

Program were scanned from print versions at a resolution of 2136 dpi and were rectified to the UTM coordinate system used by National Agricultural Imagery Program photos. We used 10 control points and ArcGIS 10.2's default projective transformation for rectification; Root Mean Square Error was always <10 (mean: 3.3). Two individuals digitized emergent vegetation, comparing results on approximately 10% of aerial photographs to ensure accuracy and consistency between digitizers. Digitization was done at a scale of 1:1500 and all patches of vegetation ≥ 5 m in width were digitized. From these data, we calculated the ratio of vegetated area to open water area within the colony site (*VegRatio*) and the percentage point change in the ratio across the observation period (*VegRatioChange*). We also used the CLUMPY index in FRAGSTATS (McGarigal *et al.* 2012) to measure interspersion of vegetation with open water (*VegClump*) and the change in interspersion across the observation period (*VegClumpChange*) at a 5-m cell size. The CLUMPY index ranges in value from -1 (maximally interspersed) to 1 (maximally clumped) and was chosen as a metric because unlike many other metrics of habitat aggregation, its value is not highly dependent on habitat abundance within the landscape (Wang *et al.* 2014).

Previous work with this dataset suggested a relationship between colony persistence and colony size in Black Terns (Wyman *et al.* 2014). Thus, we included nest abundance at the beginning of the observation period as a predictor of site abandonment (*AbPrev*).

Six variables characterized the landscape around the colony site, with reference to land cover/land use. The USGS Enhanced Historical Land-Use and Land-Cover Datasets

(U.S. Geological Survey 2010), produced from data collected between 1970 and 1985, was our source of land cover/land use data for the 1976-77 survey. The 1992 (Vogelmann *et al.* 2001), 2001 (Homer *et al.* 2007), and 2011 (Jin *et al.* 2013) versions of the National Landcover Dataset provided land cover/land use data for the 1990-91, 1998-99, and 2008-09 surveys, respectively. In recognition of known inaccuracies and problems with direct comparison among these datasets (Thogmartin *et al.* 2004; Homer *et al.* 2007), we calculated land use variables for each time period individually and only compared the resulting values rather than comparing maps directly. We calculated the proportion of land classified as developed land within a 500m buffer around the site at the end of the observation period (*Dev*) and the percentage point change across the observation period (*DevChange*). Similarly, we calculated the proportion of land classified as agricultural land within a 1000m buffer around the site at the end of the observation period (*Ag*) and the percentage point change across the observation period (*AgChange*). Buffer sizes reflected the scales at which birds are most sensitive to different land uses around wetlands as identified by Brazner and colleagues (2007). The final two landscape-level variables were distance to forest (*DistForest*) and absolute change in distance to forest across the observation period (*DistForestChange*).

At the whole lake level, we included a variable for the change in average June lake level across the observation period (*LakeLev*). Historical lake level data were obtained from the Great Lakes Water Level Dashboard (Gronewold *et al.* 2013).

Statistical Analysis

The response variable of interest was colony abandonment: “1” if the colony site was abandoned and “0” if the colony persisted through the observation period. We compared mean predictor values between abandoned and persistent colonies using Wilcoxon rank sum tests (Wilcoxon 1945), correcting for multiple testing with a Bonferroni correction (Dunn 1961). *P*-values reported in results are the Bonferroni-adjusted *p*-values. To answer the study’s primary objective, we used a binary logistic regression model (Agresti 2002) to quantify the relationship between the combined predictors and the binary response of persistence or abandonment. Continuous predictors were centered and standardized prior to model fitting. Program R (R Core Team 2014) was used to fit all models, perform model selection, and run simulations as described below.

Model selection by backwards elimination was used to simplify the full model and identify the most important predictors of Black Tern colony abandonment. Beginning with the fitted full model including all 14 predictors, we removed one predictor at a time to find the best-fitting model with 13 predictors, then removed one predictor at a time to find the best-fitting model with 12 predictors, and so on until removing another predictor did not improve on the best-fitting model from the previous step. The “best” model at each step was the model with the lowest value of Akaike’s Information Criterion (“AIC”, Akaike 1974; Burnham and Anderson 2002). Because of acknowledged inconsistencies in stepwise selection methods (Whittingham *et al.* 2006), we repeated the model selection process using forward selection, starting with a null model and adding one variable at

each step according to which produced the greatest reduction in AIC until adding another variable no longer reduced AIC.

We measured out-of-sample prediction performance for the full model and the selected reduced model by randomly dividing the dataset into subsets, withholding one subset while fitting a logistic regression model to the remaining observations, then comparing the model predictions to the observed response for the withheld cases to calculate overall classification error. The subset of data withheld consisted of either one observation (leave-one-out cross-validation) or 20% of observations (5-fold cross-validation). The division of the dataset for 5-fold cross-validation was performed randomly, so the procedure was repeated 1000 times to estimate the mean and standard error of the classification error.

In addition, we conducted a simulation study to determine potential effects of unaccounted-for association among observations from the same colony site. Twenty-two sites were represented in the original dataset by multiple observations in different time periods (45% of observations), but with over 70% of sites represented by only one observation, the data were inadequate for fitting a model that explicitly accounted for potential site-level association among observations. The data-generating model for this simulation was the fitted full model for the observed data, with the addition of a random effect of site, $\alpha_{site[j]}$:

$$\alpha_{site[j]} \sim i. i. d. Normal(0, v^2)$$

where $j = 1, \dots, 78$, indexing the 78 colony sites in the dataset. The values used for the standard deviation v were 0 (the case of no association), 0.1, 0.5, 1, 1.5, or 3. These

values on the logit scale were chosen to have a wide range of influence on predicted probability when translated to the probability scale. One hundred and one realizations of the binary response variable were generated from this model using the predictor values associated with the 101 observed responses. This process was repeated to create a total of 100 simulated datasets for each value of ν .

For each simulated dataset, we used backwards elimination to select a reduced model as described for the observed dataset. We calculated overall 5-fold cross-validation error (100 iterations per dataset) and leave-one-out cross-validation error when fitting the full model (without random effect) and the selected reduced model. Means and standard errors were calculated for the errors at each value of ν .

RESULTS

Characteristics of Black Tern Colony Sites in the U.S. Great Lakes

Abandonment of Black Tern colony sites was considerably more common than colony persistence over decadal observation periods between 1976 and 2009; 71% of observations ended in abandonment. Colony sizes at the start of the observation period ranged from one to 60 nests. Abandoned colony sites had significantly fewer nests at the beginning of the observation period compared to persistent colonies (mean: 8 nests versus 14 nests; $W = 1457$, $p = 0.021$).

The ratio of vegetation to open water at Black Tern colony sites at the end of the observation period ranged from no vegetation to almost completed vegetated (0-97%). Vegetation-to-open water ratios decreased at most by 52% or increased at most by 67%

over the decadal observation period. Vegetation clumpiness at the end of the observation period ranged from 0.59 to 0.99 on the CLUMPY index; change over the observation period ranged from a decline of 0.3 in the value of the index to an increase of 0.3. The average area and distribution of vegetation within colony sites were not significantly different ($p > 0.1$) between abandoned and persistent Black Tern colonies, nor were the changes in these variables over the observation period significant ($p > 0.1$).

Overall, agricultural area within 1 km of coastal wetland colony sites ranged from 0% to 57% of land area around the colony site. Colonies that persisted had a mean of 15% agricultural area, while colonies that were abandoned had a mean of only 5% agricultural area, a significant difference ($W = 1428, p = 0.029$). Although the mean amount of developed land within 500 m of colony sites was not substantially different between abandoned and persistent colonies ($p > 0.1$), the maximum amount of developed land area near persistent colonies was 13%, compared to a maximum of 32% near abandoned colonies. There was a wide range of distances to forest represented among Black Tern colony sites, but more than half of sites were located immediately adjacent to woody vegetation.

Predictors of Black Tern Colony Persistence

The full model included 14 variables with hypothesized relationships to Black Tern colony persistence (Table 6), representing habitat at the colony site, landscape around the site, and how those spaces changed over the observation period; abundance of Black Terns at the beginning of the observation period; change in lake level over the

observation period; geographic location; and when the observation occurred. Overall classification error for the full model was $27.1 \pm 2.6\%$ (mean \pm SE) using 5-fold cross-validation and 25.7% using leave-one-out cross-validation.

Using backwards elimination with AIC, the selected model for Black Tern colony persistence included the predictors of lake (*Lake*), survey (*Survey*), tern abundance at the start of the observation period (*AbPrev*), change in vegetation clumpiness (*VegClumpChange*), and proportion of land within 500m of the colony site that was classified as developed (*Dev*; Table 7). An identical model was selected when using forward selection as opposed to backwards elimination. Overall classification error for this model was $20.4 \pm 2.1\%$ (mean \pm SE) using 5-fold cross-validation, and 18.8% using leave-one-out cross-validation. Colonies on Lake Michigan and Lake St. Clair were more likely to be abandoned than colonies on Lake Huron or Lake Ontario. Abandonment also became more likely in later survey periods. Higher abundance of Black Terns at the start of the observation period (*AbPrev*) reduced the probability of colony site abandonment (Fig. 7). Sites where the vegetation distribution became more clumped over the observation period (*VegClumpChange*) were more likely to be abandoned (Fig. 8), as were sites with a higher proportion of developed land within 500m of the site (*Dev*; Fig. 9).

Simulation Study

Smaller models were selected by backwards elimination and AIC when there was greater association among simulated responses from the same site (Table 8). With no

association among responses, the selected model had 11 predictors on average, compared to the data-generating model's 14 predictors. When association among responses was potentially most extreme ($v = 3$), the selected model had an average of 8 predictors.

Overall classification error increased with an increase in variability of the association among simulated responses from the same site (Table 9). Even though data were generated from the full model, the selected reduced model yielded reasonably low cross-validation error, lower than the cross-validation error of the full model.

DISCUSSION

Predictors of Black Tern Colony Persistence

Black Tern abundance, change in the clumpiness of vegetation at the breeding site, and developed land use around the colony site were useful predictors of Black Tern colony persistence according to the reduced model (Table 7). These results agree with prior work showing that larger waterbird colonies are more likely to persist over time (Buckley and Buckley 1982; Kelly *et al.* 2007; Wyman *et al.* 2014) and that Black Terns tend to breed where vegetation density is moderate (Hickey and Malecki 1997; Naugle *et al.* 2000). Indeed, one of the hypothesized reasons for abandonment of colony sites in Great Lakes coastal marshes is the spread of invasive wetland plant species that grow at high densities (Matteson *et al.* 2012). Invasive cattail (*Typha X glauca*), common reed (*Phragmites australis*), and reed canary grass (*Phalaris arundinacea*), are all widely distributed throughout the Great Lakes and form dense monotypic stands (Trebitz and Taylor 2007). Although Black Terns nest on floating substrates, emergent wetland

vegetation around the nest site functions to camouflage the nest and protect it from wind and waves (Shuford 1999). The dense stands formed by the above-named invasive plants do not have the natural gaps that provide Black Terns with protected nest sites while still preserving access to adjacent open water for foraging.

Land use played an interesting role in differentiating persistent colonies from abandoned ones. According to the selected reduced model, the proportion of land in developed land use within 500 m of the colony site was related to high rates of Black Tern colony abandonment. The importance of land development as a predictor of colony abandonment was an expected result because human development is associated with degradation of foraging resources in Great Lakes coastal marshes (Brazner 1997; Brazner *et al.* 2007; Webb 2008) and another recent study in the southern Great Lakes basin showed a negative relationship between Black Tern site occupancy and development at the 3-km scale (Tozer 2016). Although agricultural land use was not included in the best-fitting model, it was one of the few characteristics for which mean values differed significantly between persistent and abandoned colonies. Persistent colonies had a higher proportion of surrounding land in agriculture than abandoned colonies. This result was surprising because agricultural land use can reduce water quality and foraging resource quality in adjacent wetlands (Beintema 1997; Crosbie and Chow-Fraser 1999), and in agricultural landscapes, Black Terns are more likely to occur in areas with higher percentages of untilled grassland relative to row-crop agriculture (Naugle *et al.* 1999b; Naugle *et al.* 2000). One possible explanation for this result is that agricultural land use at the 1-km scale is negatively correlated with other land covers or land uses that are even

less beneficial to Black Terns, although agricultural land use at the 1-km scale was not correlated with developed land use at the 500-m scale in this study. On the other hand, we did not distinguish between pasture or hay fields and row crops in land use classification for the purposes of this study, so it is possible that the terns were locating near the more grassland-like agricultural areas and not near row-crop agriculture, in agreement with previous research (Naugle *et al.* 1999b; Naugle *et al.* 2000).

Geographic location and time period were also included in the reduced model as predictors of Black Tern colony abandonment. These effects were not surprising given strong geographic and temporal patterning of the observed colony abandonments (Cuthbert and Wires 2013). Interestingly, lake level change did not appear in the chosen model. This result suggests that neither the geographic nor the temporal patterning of abandonment can be explained simply by changing mean water levels, even though nesting Black Terns are known to be sensitive to water levels (Gilbert and Servello 2005; Steen *et al.* 2006; DesGranges *et al.* 2006). It is possible that the effect of lake level, in this case, acts indirectly on Black Terns through its influence on vegetation in coastal wetlands. Influences on vegetation may include succession when water levels decline or maintenance of plant diversity through moderate water-level fluctuation (Keough *et al.* 1999; Wilcox and Nichols 2008; Lishawa *et al.* 2010).

Model Performance and Assumptions

The analysis presented here made assumptions about the dataset, but we did not attempt to check these assumptions formally because the data could not be grouped by

predictor values. Instead, we judged model performance in terms of cross-validation error. The reduced model was able to correctly classify a response based on predictor values approximately four times out of five, while the full model was able to correctly classify a response based on its predictors approximately three times out of four. These rates of classification error indicate good predictive ability for models of observational data.

The assumption of independence among observations was violated in this dataset; multiple observations were recorded from some sites and the binomial logistic regression model used did not account for potential non-independence of observations from the same site. Including a random effect for site would have allowed the model to account for such association, but we did not have adequate data to fit such a model. The simulation study showed that association among observations from the same site can affect model selection and predictive abilities. The effect on model selection was substantial; high variability in association among observations led to reduced models with as few as 8 predictors, compared to the data-generating model with 14 predictors. Because the full model was the data-generating model, if our model selection procedure were selecting the true model, it should have selected all 14 predictors, especially where $\nu = 0$. Higher variability in association among same-site observations also yielded higher overall cross-validation error, although mean overall cross-validation error remained under 25% for the selected reduced model except when $\nu = 3$. Even though the model selection procedure was not finding the true model, it was selecting a model that could still perform well in

terms of classification accuracy, likely because selection removed some of the noise introduced into the dataset by predictors with minimal association with the response.

Imperfect detection is now a widely acknowledged source of error in surveys of unmarked individuals (MacKenzie *et al.* 2006; Royle and Dorazio 2008). The Great Lakes Colonial Waterbird Survey was initiated in the 1970s before measurement of detection probability was commonly incorporated into biotic surveys. Not surprisingly, then, the survey methodology does not include the repeat visits to a site that are the most direct way to measure detection (MacKenzie *et al.* 2006). We did not account for imperfect detection in modeling Black Tern colony persistence, but believe our results to be sound for multiple reasons. First, we were only interested the process of site abandonment, so the sites included in the dataset were those known to have Black Terns and site-level detection was not an issue. Second, Black Tern detection probability is very high, over 95% for only five minutes of observation by two individuals (Shealer and Alexander 2013). Black Tern surveys in the U.S. Great Lakes commonly exceed these minimum requirements for high detection, so it is very unlikely that persistent colonies were not detected at the end of the observation period. Thus, imperfect detection likely had little impact on the results of the present study.

Conclusions

The results of this study suggest that conservationists and managers can reduce probabilities of Black Tern colony abandonment by focusing effort on two characteristics of colonies: Black Tern abundance and vegetation clumpiness within the colony site.

From a management perspective, the most important activity to preempt colony abandonment is vegetation management to maintain appropriate spatial distribution of vegetation. Black Terns respond well to vegetation management and will readily colonize restored wetlands (Delehanty and Svedarsky 1993). Management techniques successfully used for Black Terns include herbicide application (Linz *et al.* 1994) or rotating marshes through a cycle of drawdown and reflooding where hydrologic management is an option (Shuford 1999). In the Great Lakes, managers should focus especially on restoring native emergent vegetation and containing or eradicating invasive plants such as hybrid cattail (*Typha x glauca*) and the invasive genotype of common reed (*Phragmites australis*) that rapidly form dense stands once established (Tulbure *et al.* 2007; Mitchell *et al.* 2011). Management of these plants will likely require extensive resources as multiple treatments improve management outcomes (Carlson *et al.* 2009); potential for using harvested exotics as biofuel (Lishawa *et al.* 2015) may increase cost-effectiveness in the future.

From a land conservation perspective, the greatest focus should be given to colony sites that host a large number of terns and to minimizing development activities around those colonies. The St. Clair River delta is one example of a location where Black Terns consistently nest in high numbers within the U.S. Great Lakes (145-400 pairs estimated in recent years; C. Putnam, personal communication) and encounter intense pressure from development (Albert 2003). The decline of Black Terns in the Great Lakes region has been severe, and although the causes are still not fully understood, promoting the persistence of the remaining colonies is an important early step in population recovery.

CHAPTER 4

VALIDATION OF LANDSCAPE SUITABILITY INDICES FOR BLACK TERNS
(*CHLIDONIAS NIGER*) IN THE U.S. GREAT LAKES REGION

Despite maintaining a broad geographic distribution across North America, the marsh-nesting Black Tern (*Chlidonias niger*) has experienced significant declines in abundance over the past half century, particularly in the eastern portion of its range (Peterjohn and Sauer 1997; Crewe *et al.* 2005; Matteson *et al.* 2012; Cuthbert and Wires 2013). The Great Lakes Marsh Monitoring Program has estimated the population trend in the Great Lakes basin at -10.5% annually between 1995 and 2012, the greatest decline of all 19 obligate or primarily marsh-nesting bird species monitored by the program (Tozer 2013). The number of colony sites occupied by Black Terns in the Great Lakes region is also in decline (Matteson *et al.* 2012; Cuthbert and Wires 2013). Congregation of Black Terns at progressively fewer breeding sites despite, in some cases, stabilizing local population size (Matteson *et al.* 2012) suggests limited availability of suitable breeding habitat in the region, and many scientists agree that wetland habitat loss and degradation present a major challenge for Black Tern conservation (Heath *et al.* 2009). Habitat problems suggest a very different approach to management for this species than if the decline is viewed as resulting from low survival or fecundity.

The Black Tern's dramatic decline prompted designation of the bird as a focal species for habitat protection and restoration by the Upper Mississippi River and Great Lakes Region Joint Venture in 2007 ("UMGLJV", Soulliere *et al.* 2007). The UMGLJV set a goal to restore or enhance at least 4,750 ha of additional breeding habitat for the species by 2017 (Soulliere *et al.* 2007) and is currently updating these habitat objectives for future years (L. Wires personal communication). To help direct habitat conservation, restoration, and enhancement on a regional scale, the UMGLJV developed a landscape

suitability index to predict landscape suitability for Black Terns across the region (Table 10, Soulliere *et al.* 2007). Because Black Terns typically forage over open water and nest among stands of emergent vegetation (Heath *et al.* 2009), the index predicts suitability on the basis of whether open water and/or emergent vegetation are present at a wetland, as well as wetland area. To our knowledge, the UMGLJV's index is the only habitat suitability index or landscape suitability index to exist for decision-making regarding Black Terns.

Landscape-scale decision-making tools can be extremely valuable for rapidly prioritizing habitat projects over a large region. Their value is especially great for a rare and mobile species like the Black Tern that can quickly colonize restored wetlands (Delehanty and Svedarsky 1993) and whose absence from a wetland does not indicate lack of potential for future use. Furthermore, Black Terns are known to be responsive to landscape features at scales as great as 100,000 ha in prairie ecosystems (Brown and Dinsmore 1986; Naugle *et al.* 2000; Forcey *et al.* 2014), and failure of local nest-site selection models for Black Terns to be transferable to other landscapes (Hickey and Malecki 1997) emphasizes the role of landscape in Black Tern habitat suitability. From a logistical standpoint, a major benefit of the UMGLJV's landscape suitability index is its sole reliance on remotely-sensed and freely-available land cover/land use data as input, which makes this tool accessible to anyone with a moderate understanding of geographic information systems (Soulliere *et al.* 2007). The major drawback of the UMGLJV's landscape suitability index is that its design was based on expert opinion and literature

without any local field studies or validation to determine its performance ability (B. Potter personal communication).

To ensure that the UMGLJV's landscape suitability index can appropriately direct conservation and restoration priorities, we conducted surveys across the Great Lakes region to validate the UMGLJV's landscape suitability index (hereafter, the "existing index"). We then developed and similarly tested an "alternative index" by relating field survey data on Black Tern occupancy in the Great Lakes region to a wide variety of remotely-sensed landscape predictors. Our ultimate objective was to compare the performance of the existing and alternative indices to identify the highest-performing index and provide decision makers with a valid tool for future regional-scale Black Tern conservation planning.

METHODS

Study Area

Our study area included inland as well as coastal wetlands in eastern Minnesota (to the western boundary of the UMGLJV region), Wisconsin, Michigan, and northern and western New York (to the boundary of Bird Conservation Region 13 (NABCI 2011); Fig. 10). Black Terns are particularly rare in the states bordering the Great Lakes to the south (Illinois, Indiana, Ohio, and Pennsylvania), so these states were excluded from the study area to increase probability of Black Tern site occupancy to a level more amenable to statistical analysis.

Field Surveys

We used the 2006 version of the National Land Cover Dataset ("NLCD", Fry *et al.* 2011) in 2013 and the 2011 version of the NLCD (Jin *et al.* 2013) in 2014 to identify all 30m x 30m cells of emergent herbaceous wetland or open water habitat in the study area. Cells of the same type sharing at least one corner were aggregated to define individual wetlands. "Wetland complexes" were defined as areas where regions of cells of the open water class shared at least one corner with regions of cells of the emergent wetland class. Spatial analyses throughout the present study were performed using ArcGIS 10.1 (Esri, Redlands, California, USA).

In 2013, all wetlands (emergent herbaceous, open water, or wetland complex) identified using the 2006 NLCD were classified according to the existing index (Table 10). Within each category of the index, wetlands were selected at random to be potential survey sites. Sites were eliminated if the classification using the NLCD was obviously mismatched with satellite imagery of the site from Google Earth (Google, Mountain View, California, USA), if located >1 mile from the nearest road, if located within 8km of another site (to minimize spatial autocorrelation based on the foraging radius of Black Terns around their colonies, Chapman Mosher 1986), or if permission to access the land could not be obtained from the land owner. We ensured that survey sites were approximately evenly distributed among index categories, with ≥ 2 sites per category in each state and each Bird Conservation Region (as an indicator of ecoregion, NABCI 2011) in the study area.

Field teams of 2 observers surveyed 60 sites between June 3 and July 11, 2013. The default survey strategy was steady travel by kayak along the perimeter of open water while looking for Black Terns. If the site had no open water or was otherwise inaccessible to kayaks, surveys were conducted on foot or from a vantage point that offered a good view of the entire wetland. Surveys lasted between 12 and 346 minutes, depending on the size of the site and the survey strategy. Black Tern site occupancy detection probability is >95% for only 5 minutes of observation by 2 observers (Shealer and Alexander 2013). Surveys were not conducted in rain or in wind >25 mph. If Black Tern nesting was suspected in the course of a survey, observers attempted to confirm nesting on the basis of (1) aggressive adult behavior towards intruders (the observers themselves or other wildlife), (2) presence of a nest with eggs, (3) presence of Black Tern chicks, or (4) observation of adults carrying food and landing in the vegetation. Observers also noted the presence or absence of monotypic stands of *Phragmites australis* within the wetland because of concerns that *P. australis*, which has been expanding its range in the Great Lakes region (Tulbure *et al.* 2007), is not suitable habitat for Black Terns despite its similarity to suitable land cover from the perspective of the NLCD (C. Deloria-Sheffield and G. Soulliere, personal communication).

Final sample size in 2013 was 58 sites; upon visitation, one site did not match any category of the existing index and another could not be surveyed due to high water conditions. Field crews also surveyed 21 known or suspected Black Tern colony sites in 2013 to inform alternative index development (see “Methods: Alternative Index

Development”). Regional experts on Black Terns provided locations of these sites, and survey procedures were the same as for randomly selected sites.

After alternative index development (see next section), a second set of 79 randomly-chosen survey sites was visited between June 3 and July 10, 2014, using the same survey methods as those used in 2013. Classification of regional wetlands into the categories of both the existing and alternative indices were obtained using the 2011 edition of the NLCD (Jin *et al.* 2013). Forty-five of the visited sites had been randomly selected with respect to alternative index categories, and 34 sites had been randomly selected with respect to existing index categories, although all sites were eventually classified according to both indices.

Alternative Index Development

We used the 2013 survey data from randomly-selected sites as well as known Black Tern colony sites to investigate the contributions of various remotely-sensed variables to prediction of Black Tern occupancy. Consideration was given to a broad suite of landscape attributes that have potential to affect breeding or foraging habitat quality and quantity, food resources, or predation rates (Table 11). We quantified these attributes for all randomly selected survey sites and known Black Tern colony sites using the 2006 NLCD (Fry *et al.* 2011) and the National Wetland Inventory (“NWI”, Cowardin *et al.* 1979). Multiple scales of effect were considered for most landscape predictors, following Brazner and colleagues (2007) except where the foraging radius of Black Terns (2 km average, 4 km extreme, Chapman Mosher 1986) was believed to be relevant to the

effect. We also considered variables related to survey effort and timing to confirm that these did not influence detection of Black Terns or their colonies. As a preliminary step to reduce multicollinearity, we used univariate logistic regression models, implemented in Program R (R Core Team 2013), to identify the scale at which a given landscape predictor best predicted Black Tern presence. The best scale was the one used as the covariate in the model with the smallest value for Akaike's Information Criterion ("AIC", Burnham and Anderson 2002) across all models for that landscape variable.

After identifying appropriate scales for each landscape effect, we used conditional random forest classification (Breiman 2001; Hothorn *et al.* 2006a) to determine the most important predictors of Black Tern presence, implemented with the 'party' package (Hothorn *et al.* 2006a; Hothorn *et al.* 2006b; Strobl *et al.* 2007; Strobl *et al.* 2008) in Program R (R Core Team 2013). The algorithm was run for 5,000 trees with 5 variables considered at each node to enhance stability of results. Performance of the random forest classifier was evaluated using the area under the receiver operating characteristic curve ("AUC", Hanley and McNeil 1982). Poor classifiers, performing no better than random, have $AUC \approx 0.5$. A perfect classifier has $AUC = 1$.

Once the top predictors were identified, the alternative index was further adjusted to enhance ease of use. We eliminated the third-best predictor of the top 4 to reduce redundancy (see "Results: Alternative Index") and substituted an absolute area calculation for a proportional area calculation. Continuous variables were discretized by constructing a single conditional inference tree to visualize the best splits in these variables (Hothorn *et al.* 2006a). To reduce bias due to non-random sampling, known

Black Tern breeding sites were given half the weight of random survey sites in this procedure. Random forest classification was re-run twice, once with the reduced set of continuous variables and once with the discretized variables, to confirm that the classification still performed well with these modifications.

Statistical Comparison of Indices

All statistical analyses were performed in Program R (R Core Team 2014). Ridge-penalized binomial logistic regression models of Black Tern presence were fit to the dataset of randomly-selected survey sites from 2014 ($n = 79$) using one of the 2 indices as the predictor. The penalty component of the objective function to be minimized in model-fitting was:

$$\frac{\lambda}{2} \sum_{j=2}^p \beta_j^2,$$

where p is the number of coefficients in the fitted model and β_j is the j -th coefficient. Newton's method was used to optimize the objective function for each model fit. The criterion used for choosing the penalty parameter λ was the value of λ that produced the minimum cross-validation error when fitting the ridge-penalized binomial logistic regression model. When multiple values of λ led to the same minimum cross-validation error, the minimum of these λ values was selected. Cross-validation error was estimated as the proportion of responses incorrectly predicted when a model was fit to half the dataset, reserving the other half for model testing. Values considered for λ included powers of 10 from -8 to 8, in increments of 0.1.

Predictive abilities of each model were assessed by randomly splitting the dataset in half, fitting the ridge-penalized binomial logistic regression model with the chosen λ to the first half, then predicting the response of Black Tern colony presence for the other half of the dataset using the wetland score from the index in question. A prediction of “success” was defined as any predicted probability of success >0.2 , which was a reasonable definition given the overall rarity of the species. The total number of prediction errors made was summed and divided by the total number of predictions to obtain mean prediction error. This cross-validation procedure was repeated 1,000 times to obtain an estimate of the mean cross-validation error for each model and its standard error, presented in the following section as mean \pm standard error.

RESULTS

In 2013, Black Terns were detected at a total of 3 random survey sites, all of which were confirmed as locations of breeding colonies. Black Terns were present at 18 of 22 known or expected colony sites visited in 2013. Breeding was confirmed at 14 of these sites. In 2014, Black Terns were detected at 4 survey sites, 3 of which were also confirmed as the locations of breeding colonies.

Active Black Tern colonies were located in northern and southeastern Minnesota, central and southeastern Wisconsin, and the eastern end of Michigan’s Upper Peninsula. All locations with Black Tern colonies were wetland complexes >20 ha in area, and often hundreds to thousands of hectares large. Random survey sites in our sample that were occupied by Black Terns ranged in area from 157 ha to 8,310 ha, with a mean area of

2,650 ha. In contrast, the mean area of all random survey sites in the study was 225 ha and sites without Black Terns averaged only 93 ha.

Alternative Index

The final version of the alternative index (Table 12) had 2 levels of suitability, “high” and “low,” and relied on 3 wetland attributes: area of the wetland, wetland class as defined using the NLCD, and area of forageable wetlands >10 ha within 2 km (see Table 11 for details). Although the presence of emergent vegetation according to the NWI had slightly higher variable importance than forageable wetlands (Fig. 11), the former variable was removed from the index because of its redundancy with wetland class. According to the alternative index, high suitability wetlands for Black Terns are (1) wetlands ≥ 10 ha with open water and/or emergent wetland with ≥ 500 ha of forageable wetland (open water or wetland complex) within 2 km of the site, and (2) wetland complexes ≥ 40 ha with any amount of forageable wetland within 2 km. Open water and emergent wetlands had low suitability, regardless of size, if there were <500 ha of forageable wetland within 2 km.

The random forest classifier performed exceptionally well at identifying sites that would not be occupied by Black Terns (AUC = 0.94). Little performance capability was lost when all but the 3 chosen predictors were dropped from the model (AUC = 0.92), and again when continuous predictors were discretized (AUC = 0.90).

Predictive Abilities of Existing and Alternative Indices

The fitted ridge-penalized logistic regression models closely predicted the observed proportion of successes for each category of wetland in the existing and alternative indices (Fig. 12). Cross-validation error was lower for the alternative index than for the existing index, but standard errors suggest that the difference is not meaningful (existing index: 0.07 ± 0.05 ; alternative index: 0.05 ± 0.06).

DISCUSSION

Over 2 breeding seasons, Black Terns were detected at 7 of 137 randomly-selected survey sites, with breeding colonies at 6 of these sites. Even the categories of wetland where Black Terns were most likely to occur had a predicted probability of colony presence <0.2 for each index (Fig. 12). The low detection rate for Black Tern colonies likely contributed to our inability to distinguish differences in the indices' predictive abilities. However, both indices, as well as the survey data themselves, clearly point to large wetland complexes as important Black Tern habitat, and to wetlands with no or complete vegetative cover as unsuitable. This result is logical, as wetland complexes alone provide microhabitats for both foraging and breeding.

Wetland area was the most important predictor of Black Tern occupancy (Fig. 11) and was a factor in both indices (Tables 10, 12). Black Terns have been labeled “area-dependent” because size of the breeding marsh has typically been an important predictor of site occupancy (Brown and Dinsmore 1986; Naugle *et al.* 1999b; Naugle *et al.* 2000). The existing index set the definition of “large” wetlands as 20 ha or larger, while “small”

wetlands were defined as 10-20 ha in area. The alternative index shifted the dividing line between “small” and “large” up to 40 ha. Although 40 ha may have been a good dividing point within the sample provided to the classifier, most survey sites occupied by Black Terns were much larger. The alternative index (Table 12) suggests that small wetland size can be partially compensated by an abundance of wetlands in the vicinity that can be used for foraging, a result also found by Naugle and colleagues (1999b) in the Prairie Pothole Region of the central U.S.

Several predictors were notably unimportant in predicting Black Tern occupancy. Weather, timing, and search strategy all had little relative importance in Black Tern detection (Fig. 11), reinforcing previous observations that Black Terns are easy to detect (Shealer and Alexander 2013). The presence of monotypic stands of *P. australis* was not an important predictor of Black Tern presence, either, despite the potential of its invasive genotype to change the vegetation structure of Great Lakes coastal marshes (Tulbure *et al.* 2007) and anecdotal observations that it limits Black Tern breeding habitat (Matteson *et al.* 2012). *P. australis* was not observed uniformly across the study area, being much more common at sites in New York and Michigan than in Wisconsin or Minnesota, which may have limited the predictor’s utility.

The wetland characteristics used to build the indices were drawn exclusively from remotely-sensed data to facilitate their use for regional conservation planning. Presence of *P. australis* was the one exception; large *Phragmites* stands are currently mapped along the Great Lakes shoreline (U.S. Geological Survey 2015) but not consistently elsewhere within the study area at the present time. Remote sensing allows for automated

evaluation of a large number of sites in a short time, without the resources and personnel that in-person visits would require. Because a large number of candidate variables were considered when building the alternative index, the result that it did not substantially improve predictive performance over the existing index suggests that perhaps better indices are not possible without the inclusion of site characteristics for which regional-scale remotely-sensed data are difficult or costly to obtain. Vegetation structure has played a role in Black Tern colony abandonment historically (see Chapter 3) but likely is important at a finer scale than the 30m x 30m cells in which land cover data are widely available. Similarly, remotely-sensed trophic states of water bodies are not publicly available, yet eutrophication of wetlands has been suggested as a cause of Black Tern decline in Europe through its effects on both wetland vegetation and food sources (Beintema 1997; Beintema *et al.* 2010).

The UMGLJV set a goal of restoring almost 5,000 ha of potential Black Tern habitat in the Upper Mississippi River and Great Lakes region; the indices evaluated in the present study provide valuable tools for prioritizing restoration projects to meet that and future goals. The alternative index was very good at identifying locations where Black Terns would not be present. Although Shealer and Alexander (2013) argue that models are more useful if they can identify locations where birds are present, knowing which landscapes are unsuitable puts important limits on where to invest in habitat conservation and restoration. For example, restoration of strictly emergent wetland or open water habitat, or a small wetland complex with limited foraging area nearby, is likely an unwise use of resources if Black Terns are the target of restoration. Black Tern

mobility and the current small regional population both argue for protecting and restoring high quality habitat, even if unoccupied. Such habitat may be used by Black Terns in the future and has benefits for other native wetland species in the present.

ILLUSTRATIONS

Table 1. Descriptions of agonistic behaviors observed in Double-crested Cormorants and Great Blue Herons.

Species	Behavior	Description
Double-crested Cormorant	fight over nest material	aggressive; bird takes or attempts to take nest material from another nest and elicits an aggressive response from the owner of that nest, or two birds engage in “tug-of-war” at opposite ends of a piece of nest material
	threat posture ^a	aggressive; bird leans forward with neck outstretched towards its opponent and waggles its head from side to side
	retreat	submissive; bird backs away in response to aggressive behavior by another bird
	arched neck ^b	aggressive; bird raises feathers along full length of neck and curves neck into an arched shape with bill angled downward
Great Blue Heron	fight over nest material	aggressive; bird takes or attempts to take nest material from another nest and elicits an aggressive response from the owner of that nest, or two birds engage in “tug-of-war” at opposite ends of a piece of nest material
	fluffed neck ^b	aggressive; bird raises head with bill held horizontally, raising feathers along full length of neck
	forward ^b	aggressive; bird holds wings slightly out from body, pulls neck in, raises neck plumes, then shoots bill and neck forward at another bird
	retreat	submissive; bird backs away in response to aggressive behavior by another bird

^a Full description of behavior can be found in van Tets (1965).

^b Full description of behavior can be found in Mock (1976).

Table 2. Candidate model set used to predict two response variables: the total number of interspecific plus intraspecific agonistic interactions involving the focal nest in a 30-min observation period, and count of interspecific agonistic interactions involving the focal nest in a 30-min observation period.

Model Name	Hypothesis Represented
Null	Neither species identity, nor nest density, nor habitat structure affect frequency of interactions.
Species	Only species identity affects frequency of interactions.
Density	Only nest density affects frequency of interactions.
Location	Only nest location affects frequency of interactions.
Density+Location	Nest density and location, but not species identity, affect frequency of interactions.
Species+Location	Species identity and nest location, but not nest density, affect frequency of interactions.
Density+Species	Nest density and species, but not nest location, affect frequency of interactions.
Full	Nest density, nest location, and species identity all affect frequency of interactions.

Table 3. Top models of total number of interspecific plus intraspecific interactions involving a focal nest per 30-min observation period, ranked according to Akaike's Information Criterion (AIC). K indicates number of model parameters, ΔAIC indicates difference in AIC compared with highest ranking model, and w_i indicates AIC weight of model.

Model	K	ΔAIC	w_i
Species+Location	9	0.00	0.72
Density+Species+Location	10	1.94	0.28

Table 4. Models of total number of interspecific agonistic interactions involving a focal nest per 30-min observation period, ranked according to Akaike's Information Criterion (AIC). K indicates number of model parameters, ΔAIC indicates difference in AIC compared with highest ranking model, and w_i indicates AIC weight of model.

Model	K	ΔAIC	w_i
Location	7	0.00	0.46
Density+Location	8	1.75	0.19
Species+Location	8	2.00	0.17
Density+Species+Location	9	3.75	0.07
Density	7	4.23	0.06
Density+Species	8	6.19	0.02
Null	6	6.45	0.02
Species	7	8.39	0.01

Table 5. Distribution of Double-crested Cormorants (“DCCO”) and DCCO management at colonies of 4 waterbird species in the North American Great Lakes in surveys conducted between 1976 and 2010.

	Great Blue Heron	Black-crowned Night-Heron	Ring-billed Gull	Herring Gull
Total no. colony occurrences	330	224	768	3780
No. colony occurrences with DCCO present	77	97	179	448
No. colony occurrences with DCCO management present	10	15	18	36
No. observations used to fit models ^a	501	390	1299	4761

^a Number of observations used to fit models includes 3 observations (at second, third, and fourth survey periods) from all sites occupied by the co-nesting species at least once within the 4 survey periods.

Table 6. Descriptions of variables used to predict Black Tern colony persistence.

Name	Description
<i>Lake</i>	the Great Lake or connecting waterway on which the colony site was located
<i>Survey</i>	the survey period (2, 3, or 4) in which the observation period ended
<i>AbPrev</i>	abundance of Black Terns at the start of the observation period
<i>VegClump</i>	degree of interspersion of vegetation with open water at the end of the observation period, calculated using the CLUMPY index in FRAGSTATS (McGarigal <i>et al.</i> 2012); ranges from -1 to 1
<i>VegClumpChange</i>	absolute change in the CLUMPY index over the observation period (see <i>VegClump</i>)
<i>VegRatio</i>	ratio of vegetated area to open water within the colony site
<i>VegRatioChange</i>	percentage point change over observation period in the ratio of vegetated area to open water within the colony site
<i>DistForest</i>	distance from edge of colony site to forested land cover
<i>DistForestChange</i>	absolute change in distance from edge of colony site to forested land cover over the observation period
<i>Ag</i>	proportion of land area in agricultural use within 1km of colony site
<i>AgChange</i>	percentage point change over observation period in proportion of land area in agricultural use within 1km of colony site
<i>Dev</i>	proportion of land area in developed land use within 500m of colony site
<i>DevChange</i>	percentage point change over observation period in proportion of land area in developed land use within 500m of colony site
<i>LakeLev</i>	absolute change in lake level over observation period

Table 7. Coefficient estimates and estimated standard errors for selected reduced model to predict Black Tern colony persistence, selected via backwards elimination with AIC as the selection criterion.

Predictor	Estimate \pm SE
Intercept (<i>Lake</i> = Huron, including St. Marys River)	-2.48 \pm 2.13
<i>Lake</i> = Michigan	0.86 \pm 1.01
Lake = Ontario	-3.02 \pm 0.82
<i>Lake</i> = St. Clair	0.63 \pm 1.11
<i>Survey</i>	1.38 \pm 0.66
<i>AbPrev</i>	-0.82 \pm 0.37
<i>VegClumpChange</i>	0.78 \pm 0.37
<i>Dev</i>	0.61 \pm 0.37

Table 8. Change in mean number of parameters (\pm SE) in selected model with change in magnitude of site-level effects. The selected model was the model with lowest AIC obtained through backwards elimination, starting with a full model involving 14 predictors. Data were simulated from the 14-predictor model with an additional normally-distributed random effect of “site” with standard deviation ν . The random effect was ignored in model fitting.

ν	Number of parameters
0	10.73 \pm 1.87
0.1	10.52 \pm 1.96
0.5	10.59 \pm 1.74
1	10.37 \pm 2.11
1.5	9.61 \pm 2.18
3	8.19 \pm 2.08

Table 9. Mean overall classification error for simulated colony abandonment data using 5-fold and leave-one-out cross-validation. Classification error (mean \pm SE, for 5-fold) was calculated for the full model and for a reduced model selected using backwards elimination and AIC as the selection criterion. Data were simulated from the fitted full model plus a normally-distributed random effect of “site” with standard deviation v . The random effect was ignored in model fitting on simulated data.

v	5-fold cross-validation		Leave-one-out cross-validation	
	Full model	Reduced model	Full model	Reduced model
0	0.229 \pm 0.039	0.190 \pm 0.037	0.211	0.181
0.1	0.230 \pm 0.038	0.191 \pm 0.038	0.214	0.184
0.5	0.236 \pm 0.042	0.197 \pm 0.041	0.222	0.191
1	0.248 \pm 0.044	0.211 \pm 0.043	0.235	0.206
1.5	0.274 \pm 0.044	0.231 \pm 0.044	0.262	0.223
3	0.346 \pm 0.055	0.290 \pm 0.050	0.333	0.284

Table 10. Existing landscape suitability index for Black Terns in the Upper Mississippi River and Great Lakes region, developed from literature and expert opinion (Soulliere *et al.* 2007).

Wetland Characteristics	Score
Wetland complexes ^a >20 ha (excluding Great Lakes >4 km offshore)	100
Wetland complexes 10-20 ha, <4 km from open water >10 ha	80
Emergent wetland >20 ha	60
Emergent wetland 10-20 ha, <4 km from open water >10 ha	40
Open water >20 ha (excluding the Great Lakes)	20
Open water 10-20 ha, <4 km from emergent wetland >10 ha	10

^a Wetland complexes are patches that contain both “emergent wetland” and “open water” classes from the National Land Cover Database (Fry *et al.* 2011; Jin *et al.* 2013).

Table 11. Variables considered as potential predictors of Black Tern presence.

Landscape variables were constructed using the 2006 National Land Cover Dataset ("NLCD", Fry *et al.* 2011), except where variables are noted as being drawn from National Wetlands Inventory ("NWI", Cowardin *et al.* 1979).

Variable Name	Interpretation
Latitude	Latitude coordinate of survey site
Longitude	Longitude coordinate of survey site
BCR	Bird Conservation Region in which site is located (NABCI 2011)
State	State in which site is located
Ownership	Whether site was under primarily (1) public or (2) private ownership
NLCD_Class	Land cover class in NLCD: (1) open water (class 11); (2) emergent wetland (class 95); (3) wetland complex (areas where classes 11 and 95 were contiguous); or (4) none of the above
NWI_System	System in NWI: (1) lacustrine (L1, L2), (2) palustrine (P), or (3) non-wetland
NWI_Class	Predominant class in NWI: (1) emergent (EM), (2) forest (FO) or shrub-scrub (SS), (3) unconsolidated bottom (UB), or (4) non-wetland
NWI_H2Omanage	Presence or absence of water management (dikes, etc.), according to NWI
NWI_EmPresent	Presence or absence of emergent vegetation, according to NWI
Area_in_ha	Area of site, measured in hectares

Variable Name	Interpretation
Prop_ag_5kmbuff, Prop_ag_1kmbuff	Proportion of 5 km or 1 km buffer surrounding site that was planted/cultivated
Prop_dev_1kmbuff, Prop_dev_500mbuff, Prop_dev_100mbuff	Proportion of 1 km, 500 m, or 100 m buffer surrounding site that was developed
Prop_woody_perim	Proportion of 5 m buffer surrounding site that had forest or shrub-scrub cover
Prop_nat_5kmbuff, Prop_nat_2kmbuff, Prop_nat_1kmbuff	Proportion of 5 km, 2 km, or 1 km buffer surrounding site that had natural land cover (not developed or planted/cultivated)
Prop_forage_4kmbuff, Prop_forage_2kmbuff	Proportion of 4 km or 2 km buffer surrounding site that was forageable, i.e. having open water or wetland complex land cover
OW_prop_4kmbuff, OW_prop_2kmbuff	Proportion of open water in wetland complexes in surrounding 4 km or 2 km buffer
Num_OW_4km, Num_OW_2km	Number of unique open water habitats (including open water within wetland complexes) in surrounding 4 km or 2 km buffer
Num_OWonly_4km, Num_OWonly_2km	Number of unique open water habitats (not including wetland complexes) in surrounding 4 km or 2 km buffer
Num_WC_4km, Num_WC_2km	Number of unique wetland complex habitats in surrounding 4 km or 2 km buffer
Prop_forage10_4kmbuff, Prop_forage10_2kmbuff	Proportion of 4 km or 2 km buffer surrounding site that was forageable in units >10 ha, i.e. having contiguous open water or wetland complex land cover >10 ha

Variable Name	Interpretation
OW10_prop_4kmbuff, OW10_prop_2kmbuff	Proportion of open water in wetland complexes >10 ha in surrounding 4 km or 2 km buffer
Num_OW10_4km, Num_OW10_2km	Number of unique open water habitats >10 ha (including open water within wetland complexes) in surrounding 4 km or 2 km buffer
Num_OW10only_4km, Num_OW10only_2km	Number of unique open water habitats >10 ha (not including wetland complexes) in surrounding 4 km or 2 km buffer
Num_WC10_4km, Num_WC10_2km	Number of unique wetland complex habitats >10 ha in surrounding 4 km or 2 km buffer
Visit_Day	Julian date of visit
Search_Time	Time spent searching site for Black Terns
Area_Searched	Area of site searched (often, but not always, same as total area of site)
Precipitation	Precipitation occurring during survey: (1) None, or (2) Light/variable
Wind	Wind speed during survey: (1) Calm-light breeze (0-7 mph), (2) Gentle or moderate breeze (8-18 mph), or (3) Fresh breeze (19-24 mph)
Transport_Mode	Transportation mode during survey: (1) boat, or (2) on foot
Search_Strategy	Search method: (1) travel around perimeter of site, (2) travel by another path through the site, or (3) observe whole site from a vantage point
Phragmites_Present	Presence or absence of monotypic stands of <i>Phragmites australis</i>

Table 12. Alternative model for predicting suitable Black Tern habitat, given wetlands of >10 ha of contiguous habitat that are classified in the National Land Cover Dataset (Jin *et al.* 2013) as consisting of open water, emergent wetland, or a combination of these.

Forageable buffer area	Area of wetland	NLCD Classification	Value for Black Terns
>500 ha	>10 ha	Wetland complex	High
		Open water	High
		Emergent wetland	High
<500 ha	>40 ha	Wetland complex	High
		Open water	Low
		Emergent wetland	Low
	10 - 40 ha	Any	Low

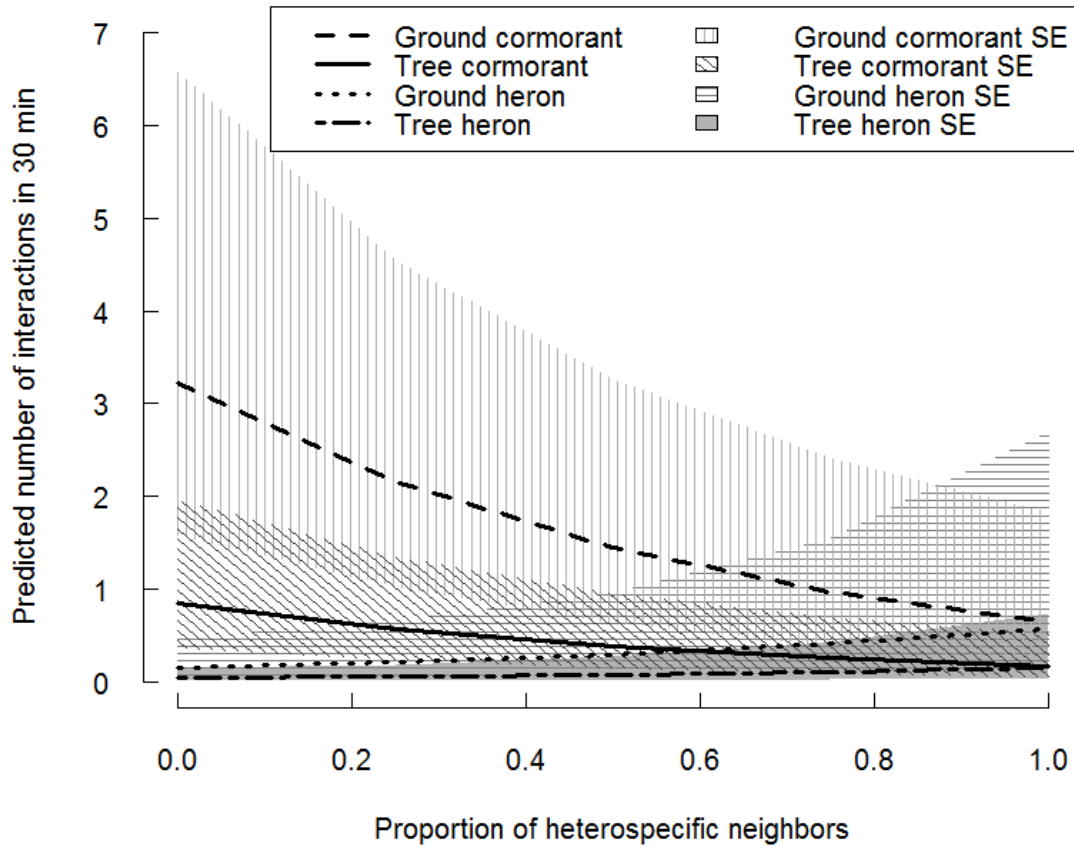


Figure 1. Predicted number of combined interspecific and intraspecific agonistic interactions (\pm SE) in 30 min for Double-crested Cormorants (“cormorant”) and Great Blue Herons (“heron”), by nest location (ground or tree) and proportion of four nearest neighbors that are heterospecifics. Predictions were calculated according to the top model in the candidate set, with date and time fixed at their medians.

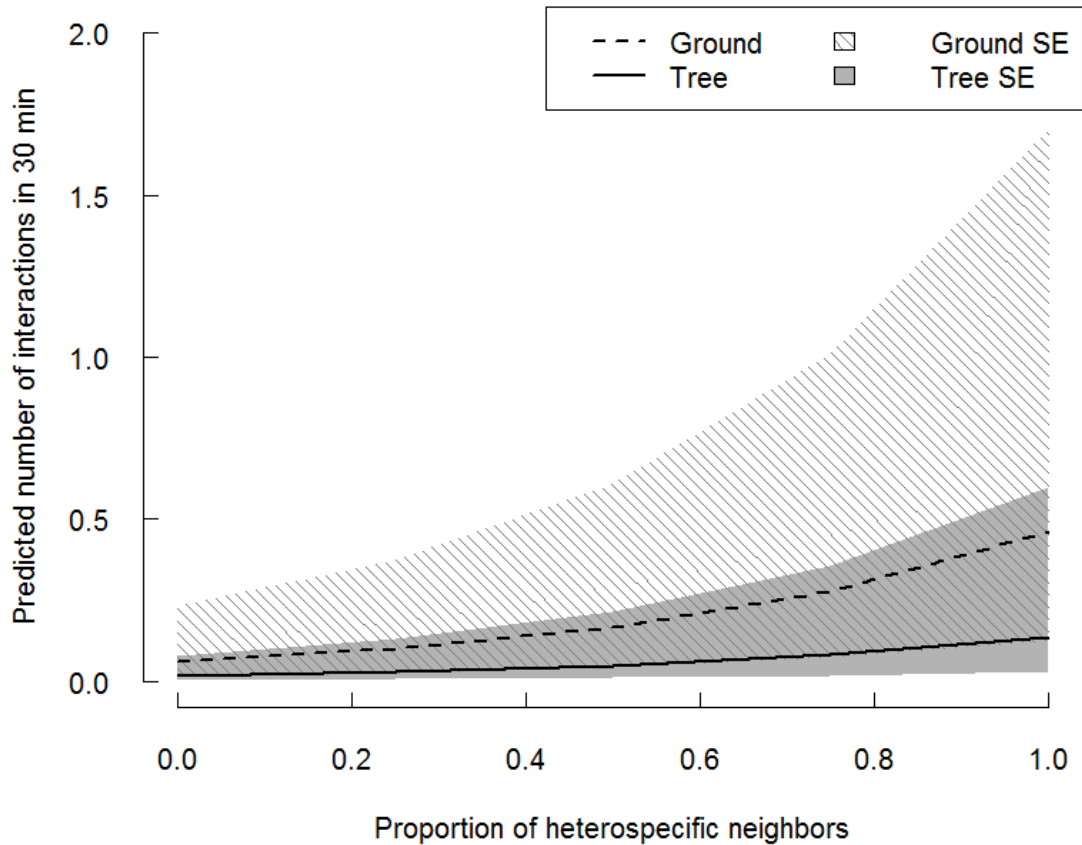


Figure 2. Predicted number of interspecific interactions (\pm SE) in 30 min involving a nest of either Double-crested Cormorants or Great Blue Herons, by nest location and proportion of four nearest neighbors that are heterospecifics. Predictions were calculated according to the top model in the candidate set, with date and time fixed at their medians.

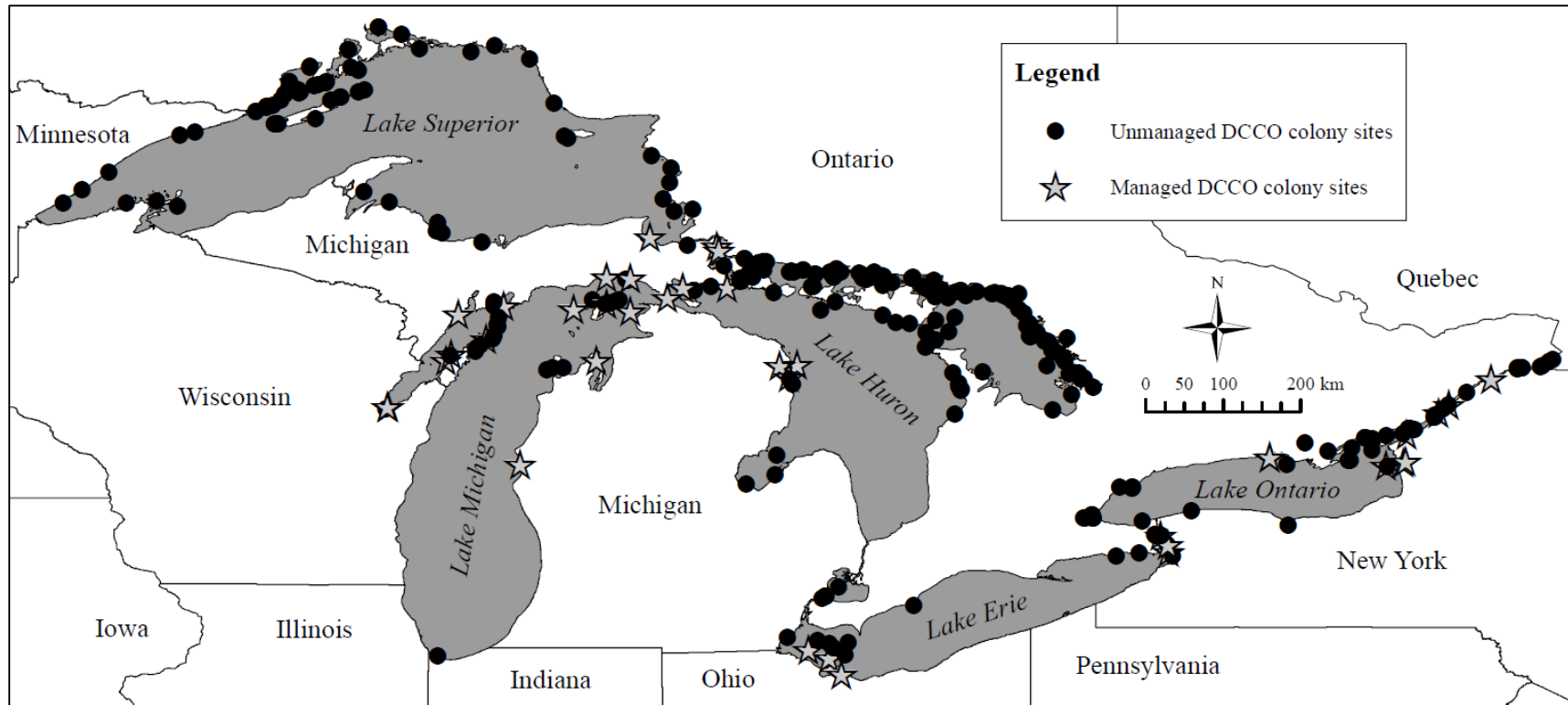


Figure 3. Double-crested Cormorant colony sites in the North American Great Lakes, as identified by the Great Lakes Colonial Waterbird Survey (Cuthbert and Wires 2013) and comparable surveys in Canada (D.J. Moore, personal communication).

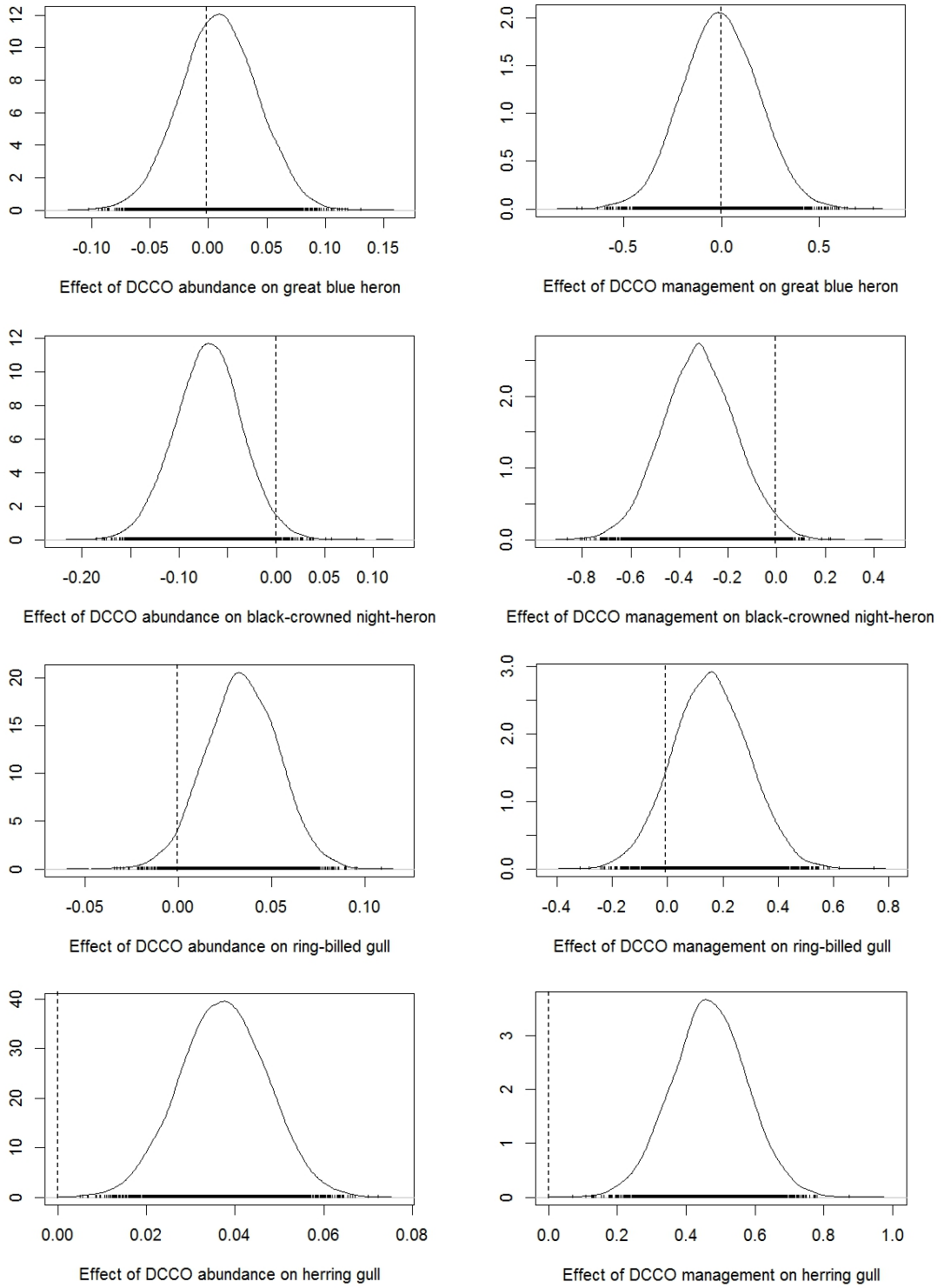


Figure 4. Estimated posterior densities for effects of DCCO abundance and presence of management on colony growth index for 4 colonial waterbird species that nest with

DCCO in the North American Great Lakes. Dotted lines show the location of 0, the value indicating no effect. DCCO abundance was scaled to have a standard deviation of 1 prior to model fitting.

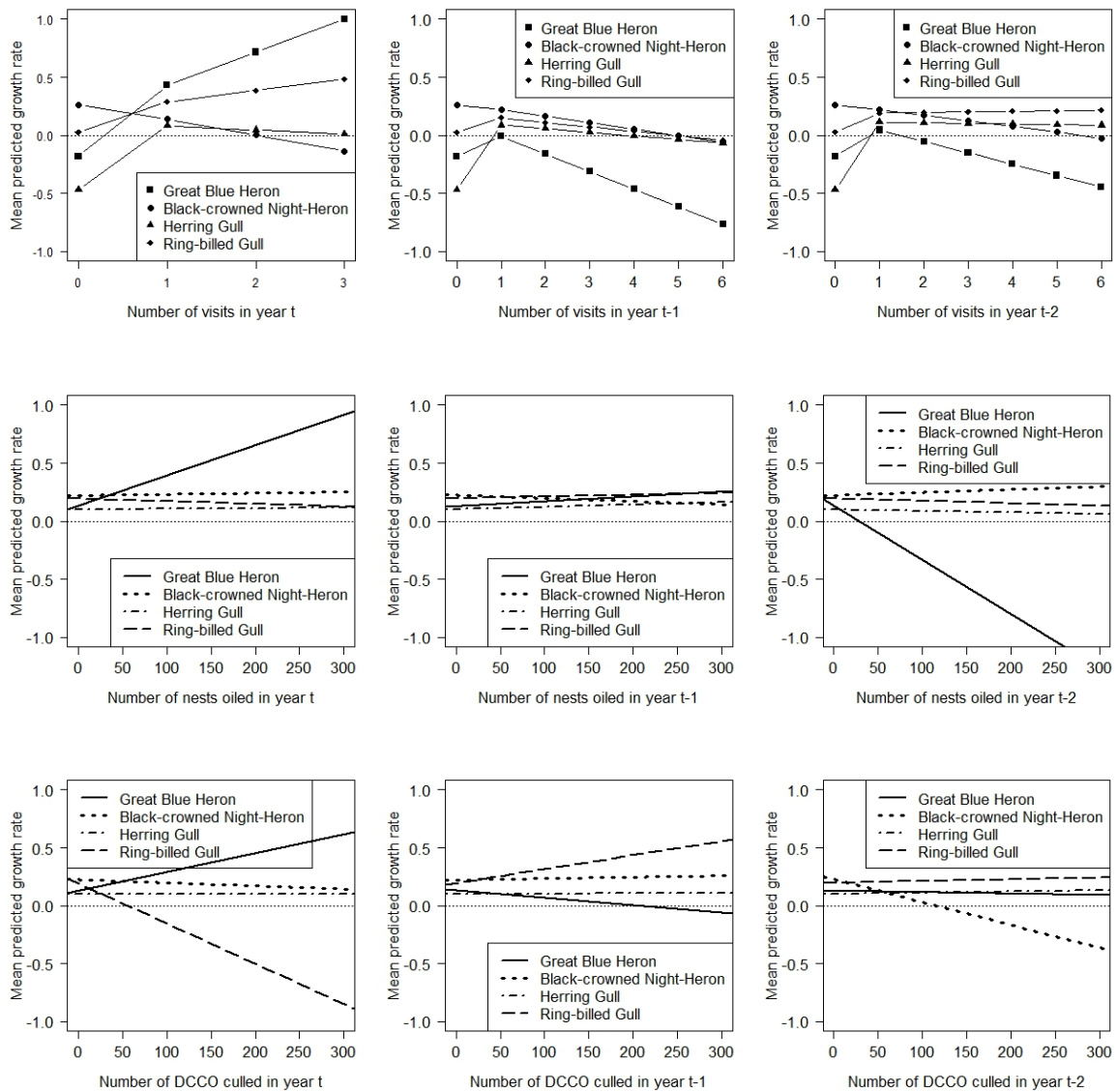


Figure 5. Mean predicted colony growth index of 4 waterbird species as a function of number of Double-crested Cormorant management visits (top), number of Double-crested Cormorant nests oiled (middle), and number of Double-crested Cormorants culled (bottom) in the year of survey and the 2 previous years. Colony growth index values were calculated for the periods between decadal surveys conducted from 1976 through 2010;

the colony growth index ranges in value from -1 to 1. Effect of presence or absence of Double-crested Cormorant management is included in predicted colony growth index value as a function of number of visits; effect of management presence was added on if number of visits was >0 . All other covariates were held constant at their median, except for Double-crested Cormorant abundance, which was held constant at the median value for sites with Double-crested Cormorants present.

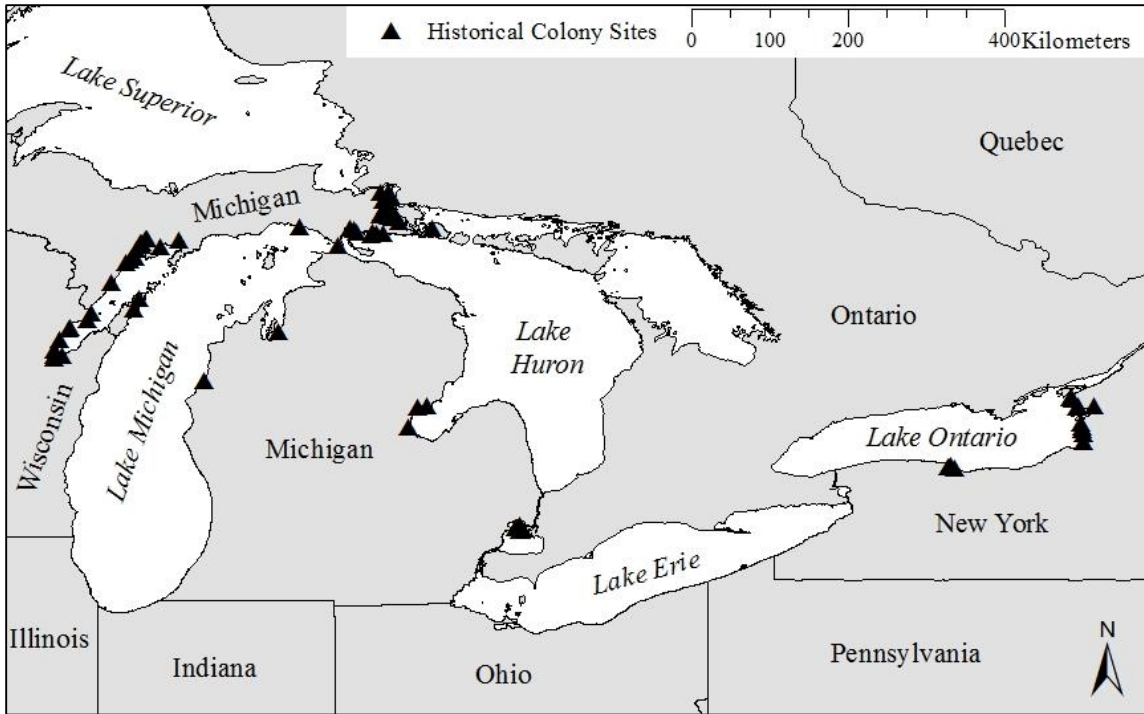


Figure 6. Locations of Black Tern colony sites on the U.S. Great Lakes 1976-2009, as reported by the Great Lakes Colonial Waterbird Survey (Cuthbert and Wires 2013).

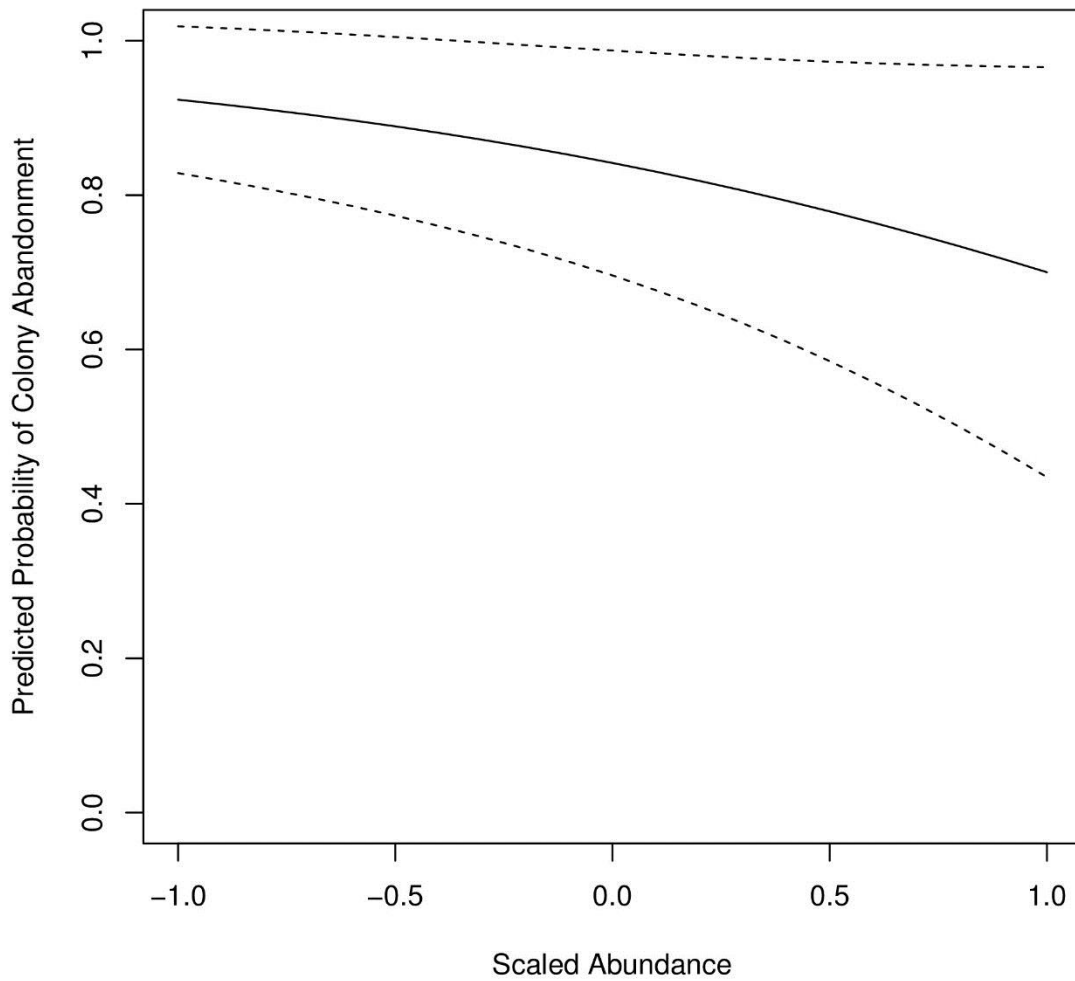


Figure 7. Predicted probability and 95% confidence intervals for colony abandonment in relation to Black Tern abundance on Lake Huron in the third survey, according to the reduced model selected by AIC. Abundance is shown on a standardized scale, where 0 represents approximately 10 terns and a difference of 1 unit represents a difference of approximately 10 terns. Remaining predictors in the model were held at their means.

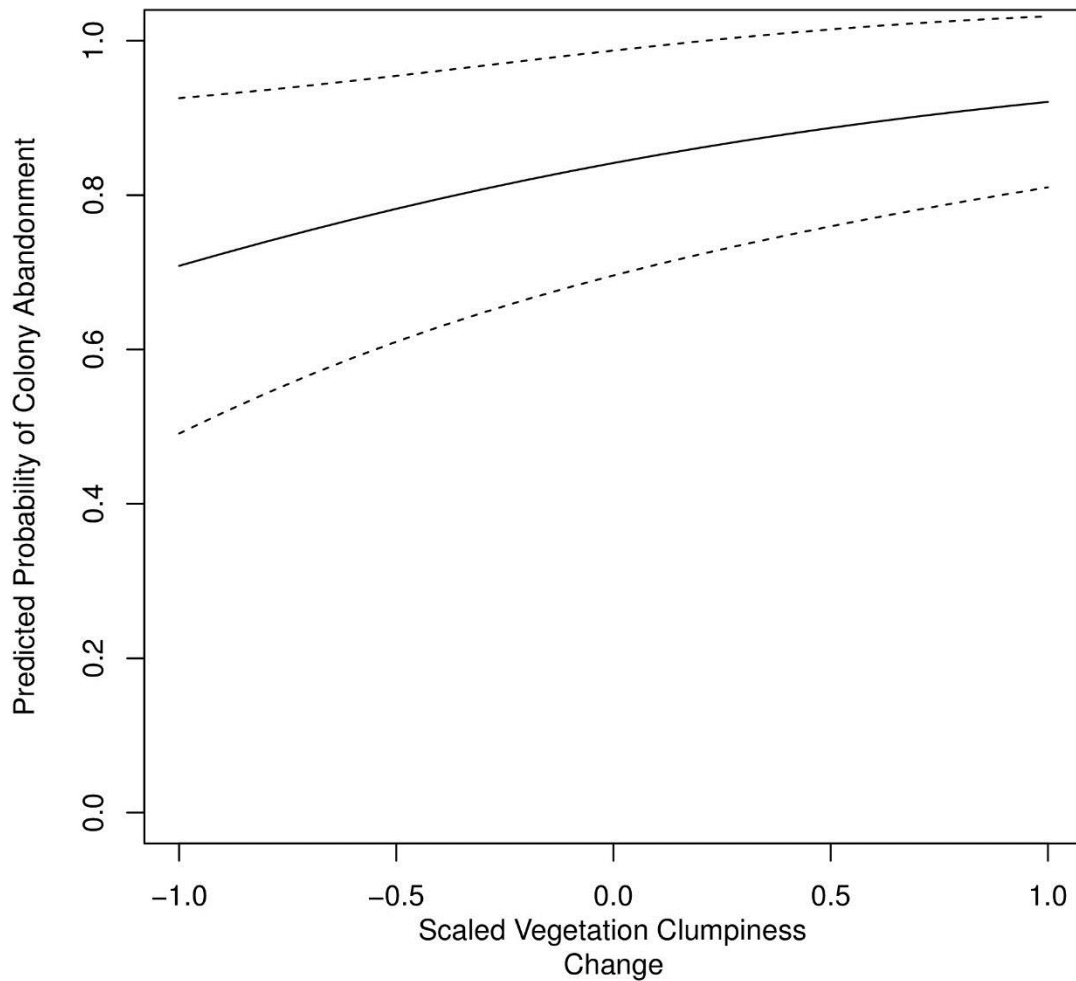


Figure 8. Predicted probability and 95% confidence intervals for colony abandonment in relation to change in vegetation clumpiness on Lake Huron in the third survey, according to the reduced model selected by AIC. Change in vegetation clumpiness is shown on a standardized scale, where 0 represents approximately no change in clumpiness, as measured by the CLUMPY index (McGarigal *et al.* 2012). A difference of 1 unit

represents a change of approximately 0.08 in the CLUMPY index, which ranges from -1 to 1. Remaining predictors in the model were held at their means.

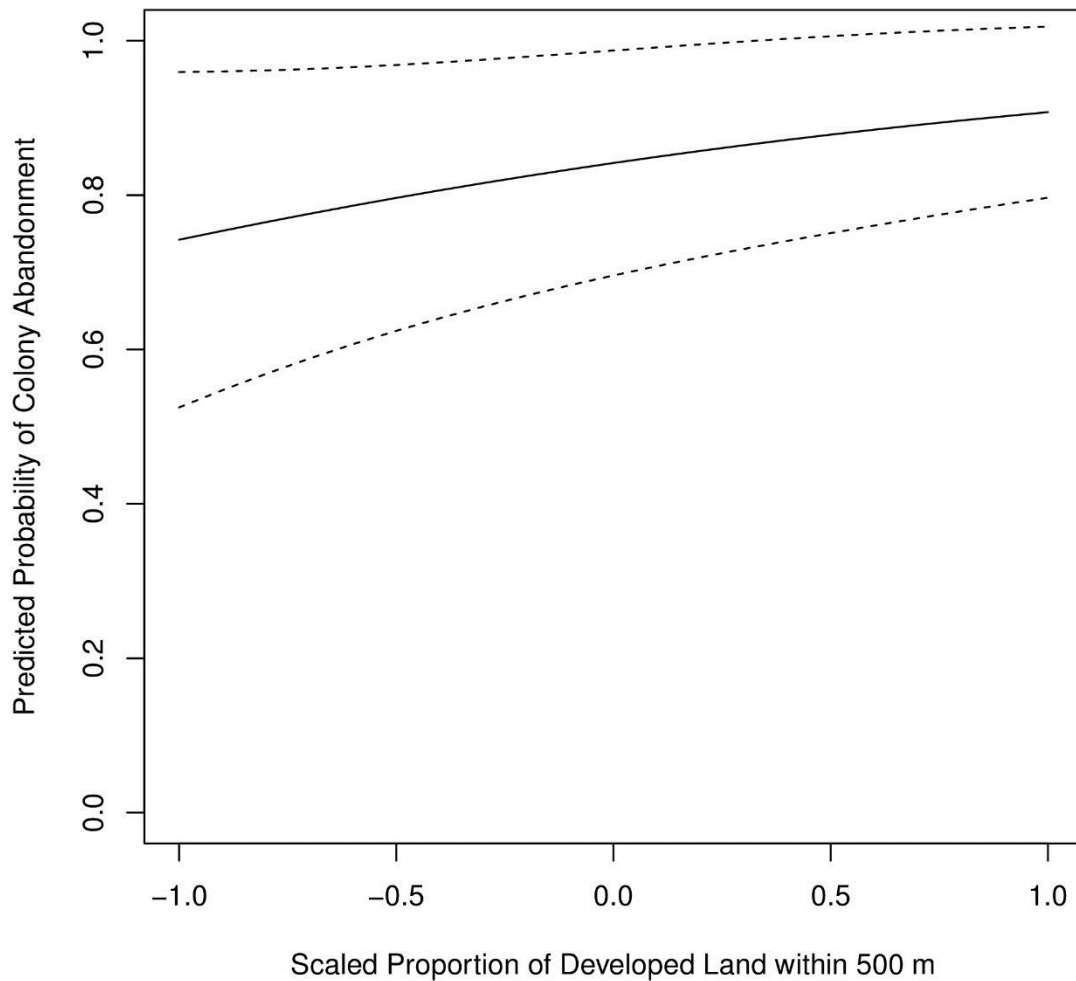


Figure 9. Predicted probability and 95% confidence intervals for colony abandonment in relation to proportion of development within 500 m of Black Tern colony sites on Lake Huron in the third survey, according to the reduced model selected by AIC. Development is shown on a standardized scale, where 0 represents approximately 6% developed land area and an increase of 1 unit indicates an additional 5% the land within 500 m of the colony site was developed. Remaining predictors in the model were held at their means.

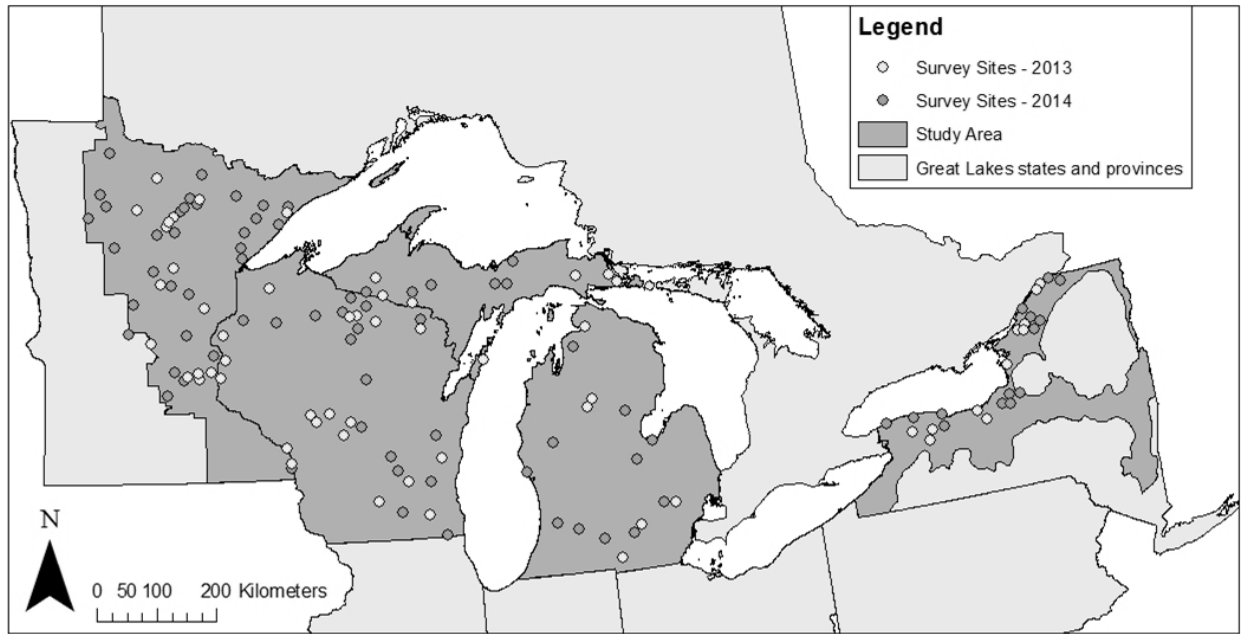


Figure 10. Study area for validation of landscape suitability indices for Black Terns developed by the Upper Mississippi River and Great Lakes Region Joint Venture (Soulliere *et al.* 2007) and by the authors. The study area included those portions of Bird Conservation Regions 12 (boreal hardwood transition), 13 (lower Great Lakes/St. Lawrence Plain), and 23 (prairie hardwood transition, NABCI 2011) located within the states of New York, Michigan, Wisconsin, and Minnesota to the western boundary of the Upper Mississippi River and Great Lakes Region Joint Venture region.

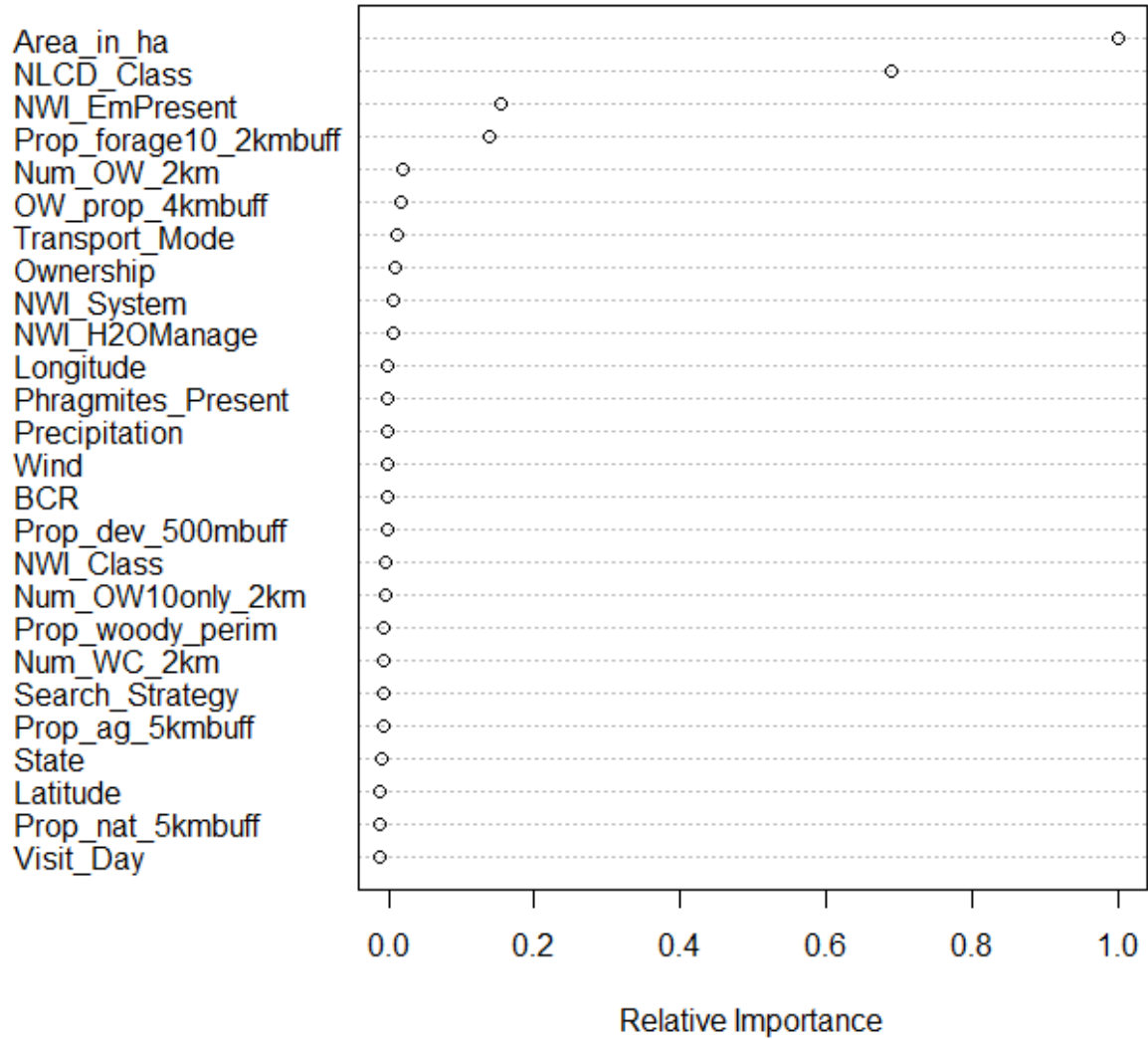


Figure 11. Relative importance of landscape variables in predicting Black Tern colony presence in the Great Lakes region. Variable definitions are provided in Table 11.

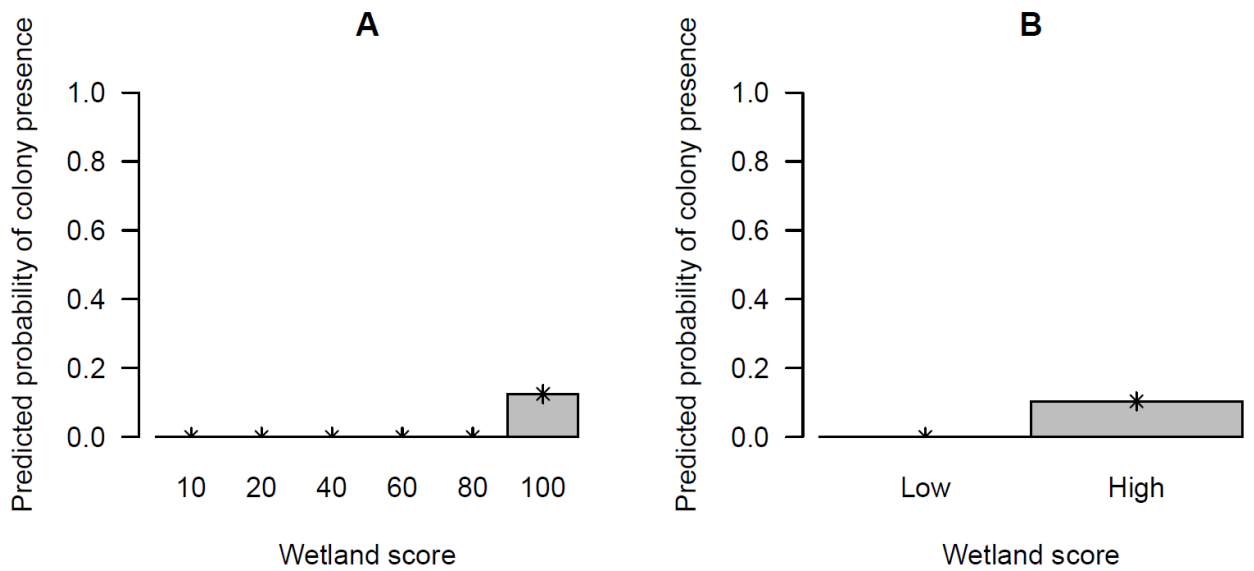


Figure 12. Predicted probability of Black Tern colony presence by wetland score, according to (A) the existing landscape suitability index (Table 10), and (B) the alternative landscape suitability index (Table 12). Bars represent predictions of the fitted ridge-penalized binomial logistic regression models. Asterisks indicate observed occupancy rate for each value of the explanatory variable, wetland score.

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APPENDIX

MODEL SPECIFICATION

Observations are indexed by i (Table 5 includes total number of observations for each species). Year t represents the final year of the period across which colony growth index was calculated and the year in which colonies were surveyed.

Model 1

Hypothesis: There is an association between co-nester colony growth index and Double-crested Cormorant (“DCCO”) abundance.

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

$$\mu_i = \beta_0 + \beta_1 * \text{floodprone}_i + \beta_2 * \text{prior growth rate}_i + \beta_3$$

$$* \text{historical species richness}_i + \beta_4 * \text{historical abundance}_i + \beta_5$$

$$* \text{other disturbance}_i + \beta_6 * \text{DCCO abundance}_i + \alpha_{\text{site}}[\text{site number}_i]$$

$$+ \alpha_{\text{lake}}[\text{waterbody}_i] + \alpha_{\text{survey}}[\text{survey period}_i]$$

$$\alpha_{\text{site}}[\text{site number}_i] \sim \text{Normal}(0, \sigma_{\text{site}}^2)$$

$$\alpha_{\text{lake}}[\text{waterbody}_i] \sim \text{Normal}(0, \sigma_{\text{lake}}^2)$$

$$\alpha_{\text{survey}}[\text{survey period}_i] \sim \text{Normal}(0, \sigma_{\text{survey}}^2)$$

Model 2

Hypothesis: There is an association between co-nester colony growth index and presence of DCCO management.

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

$$\begin{aligned} \mu_i = & \beta_0 + \beta_1 * floodprone_i + \beta_2 * prior\ growth\ rate_i + \beta_3 \\ & * historical\ species\ richness_i + \beta_4 * historical\ abundance_i + \beta_5 \\ & * other\ disturbance_i + \beta_6 * DCCO\ abundance_i + \beta_7 \\ & * presence\ of\ management_i + \alpha_{site}[site\ number_i] \\ & + \alpha_{lake}[waterbody_i] + \alpha_{survey}[survey\ period_i] \end{aligned}$$

$$\alpha_{site}[site\ number_i] \sim Normal(0, \sigma_{site}^2)$$

$$\alpha_{lake}[waterbody_i] \sim Normal(0, \sigma_{lake}^2)$$

$$\alpha_{survey}[survey\ period_i] \sim Normal(0, \sigma_{survey}^2)$$

Model 3

Hypothesis: There is an association between co-nester colony growth index and number of DCCO management-related visits made to the colony site.

$$Colony\ growth\ index_i \sim Normal(\mu_i, \sigma^2)$$

$$\begin{aligned} \mu_i = & \beta_0 + \beta_1 * floodprone_i + \beta_2 * prior\ growth\ rate_i + \beta_3 \\ & * historical\ species\ richness_i + \beta_4 * historical\ abundance_i + \beta_5 \\ & * other\ disturbance_i + \beta_6 * DCCO\ abundance_i + \beta_7 \\ & * presence\ of\ management_i + \beta_8 * visits\ in\ year\ t_i + \beta_9 \\ & * visits\ in\ year\ t - 1_i + \beta_{10} * visits\ in\ year\ t - 2_i \\ & + \alpha_{site}[site\ number_i] + \alpha_{lake}[waterbody_i] \\ & + \alpha_{survey}[survey\ period_i] \end{aligned}$$

$$\alpha_{site}[site\ number_i] \sim Normal(0, \sigma_{site}^2)$$

$$\alpha_{lake}[waterbody_i] \sim Normal(0, \sigma_{lake}^2)$$

$$\alpha_{survey}[survey\ period_i] \sim Normal(0, \sigma_{survey}^2)$$

Model 4

Hypothesis: There is an association between co-nester colony growth index and either number of DCCO nests oiled, number of DCCO culled, or both.

$$Colony\ growth\ index_i \sim Normal(\mu_i, \sigma^2)$$

$$\begin{aligned} \mu_i = & \beta_0 + \beta_1 * floodprone_i + \beta_2 * prior\ growth\ rate_i + \beta_3 \\ & * historical\ species\ richness_i + \beta_4 * historical\ abundance_i + \beta_5 \\ & * other\ disturbance_i + \beta_6 * DCCO\ abundance_i + \beta_7 \\ & * nests\ oiled\ in\ year\ t_i + \beta_8 * nests\ oiled\ in\ year\ t - 1_i + \beta_9 \\ & * nests\ oiled\ in\ year\ t - 2_i + \beta_{10} * DCCO\ culled\ in\ year\ t_i + \beta_{11} \\ & * DCCO\ culled\ in\ year\ t - 1_i + \beta_{12} * DCCO\ culled\ in\ year\ t - 2_i \\ & + \alpha_{site}[site\ number_i] + \alpha_{lake}[waterbody_i] \\ & + \alpha_{survey}[survey\ period_i] \end{aligned}$$

$$\alpha_{site}[site\ number_i] \sim Normal(0, \sigma_{site}^2)$$

$$\alpha_{lake}[waterbody_i] \sim Normal(0, \sigma_{lake}^2)$$

$$\alpha_{survey}[survey\ period_i] \sim Normal(0, \sigma_{survey}^2)$$

TABLES

Table S1. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Great Blue Heron colony growth used to examine the hypothesis that colony growth index is related to Double-crested Cormorant abundance (model 1 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.110	-1.561	1.735
β_1	effect of flood-proneness	-0.062	-0.375	0.255
β_2	effect of prior colony growth index	-0.283	-0.390	-0.174
β_3	effect of historical species richness	0.051	-0.056	0.161
β_4	effect of historical abundance	-0.097	-0.166	-0.03
β_5	effect of presence of other disturbances	-0.123	-0.294	0.049
β_6	effect of Double-crested Cormorant abundance	0.009	-0.056	0.074
σ	standard deviation of colony growth index	0.683	0.640	0.730
σ_{survey}	standard deviation of survey random effect	0.962	0.113	5.725
σ_{lake}	standard deviation of waterbody random effect	0.109	0.006	0.298
σ_{site}	standard deviation of site random effect	0.052	0.004	0.135

Table S2. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Great Blue Heron colony growth used to examine the hypothesis that colony growth index is related to presence of Double-crested Cormorant management (model 2 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.118	-2.430	2.713
β_1	effect of flood-proneness	-0.064	-0.373	0.257
β_2	effect of prior colony growth index	-0.281	-0.388	-0.175
β_3	effect of historical species richness	0.052	-0.058	0.163
β_4	effect of historical abundance	-0.097	-0.166	-0.031
β_5	effect of presence of other disturbances	-0.123	-0.296	0.052
β_6	effect of Double-crested Cormorant abundance	0.009	-0.055	0.073
β_7	effect of Double-crested Cormorant management	-0.007	-0.380	0.374
σ	standard deviation of colony growth index	0.684	0.642	0.731
σ_{survey}	standard deviation of survey random effect	1.384	0.113	11.446
σ_{lake}	standard deviation of waterbody random effect	0.112	0.007	0.313
σ_{site}	standard deviation of site random effect	0.047	0.003	0.130

Table S3. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Great Blue Heron colony growth used to examine the hypothesis that colony growth index is related to number of visits made for Double-crested Cormorant management (model 3 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	-0.208	-2.034	1.642
β_1	effect of flood-proneness	-0.042	-0.359	0.283
β_2	effect of prior colony growth index	-0.281	-0.385	-0.174
β_3	effect of historical species richness	0.046	-0.064	0.155
β_4	effect of historical abundance	-0.103	-0.171	-0.035
β_5	effect of presence of other disturbances	-0.095	-0.270	0.081
β_6	effect of Double-crested Cormorant abundance	0.007	-0.057	0.069
β_7	effect of Double-crested Cormorant management	0.323	-0.504	1.127
β_8	effect of # management visits in year t	0.052	-0.027	0.132
β_9	effect of # management visits in year $t - 1$	-0.065	-0.163	0.036
β_{10}	effect of # management visits in year $t - 2$	-0.042	-0.121	0.037
σ	standard deviation of colony growth index	0.683	0.641	0.729
σ_{survey}	standard deviation of survey random effect	0.990	0.107	5.854
σ_{lake}	standard deviation of waterbody random effect	0.105	0.007	0.288
σ_{site}	standard deviation of site random effect	0.044	0.002	0.125

Table S4. Estimated means and 0.025 and 0.975 quantiles of the posterior distributions of parameters estimated in the model of Great Blue Heron colony growth used to examine the hypothesis that colony growth index is related to cormorant management via number of nests oiled and number of birds culled (model 4 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.116	-1.829	2.025
β_1	effect of flood-proneness	-0.051	-0.375	0.281
β_2	effect of prior colony growth index	-0.290	-0.396	-0.182
β_3	effect of historical species richness	0.032	-0.076	0.143
β_4	effect of historical abundance	-0.099	-0.169	-0.028
β_5	effect of presence of other disturbances	-0.075	-0.254	0.105
β_6	effect of Double-crested Cormorant abundance	-0.005	-0.071	0.060
β_7	effect of # nests oiled in year t	0.020	-0.072	0.111
β_8	effect of # nests oiled in year $t - 1$	0.075	-0.015	0.187
β_9	effect of # nests oiled in year $t - 2$	-0.050	-0.149	0.049
β_{10}	effect of # birds culled in year t	0.142	0.002	0.280
β_{11}	effect of # birds culled in year $t - 1$	-0.108	-0.246	0.035
β_{12}	effect of # birds culled in year $t - 2$	-0.002	-0.057	0.052
σ	standard deviation of colony growth index	0.683	0.639	0.729
σ_{survey}	standard deviation of survey random effect	1.131	0.113	7.808
σ_{lake}	standard deviation of waterbody random effect	0.098	0.005	0.275
σ_{site}	standard deviation of site random effect	0.045	0.001	0.129

Table S5. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Black-crowned Night-Heron colony growth used to examine the hypothesis that colony growth index is related to Double-crested Cormorant abundance (model 1 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.372	-0.691	1.542
β_1	effect of flood-proneness	-0.042	-0.278	0.193
β_2	effect of prior colony growth index	-0.395	-0.515	-0.276
β_3	effect of historical species richness	-0.117	-0.243	0.010
β_4	effect of historical abundance	-0.083	-0.152	-0.014
β_5	effect of presence of other disturbances	-0.076	-0.231	0.078
β_6	effect of Double-crested Cormorant abundance	-0.075	-0.144	-0.009
σ	standard deviation of colony growth index	0.629	0.583	0.676
σ_{survey}	standard deviation of survey random effect	0.612	0.027	4.655
σ_{lake}	standard deviation of waterbody random effect	0.059	0.002	0.184
σ_{site}	standard deviation of site random effect	0.054	0.003	0.151

Table S6. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Black-crowned Night-Heron colony growth used to examine the hypothesis that colony growth index is related to presence of Double-crested Cormorant management (model 2 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.692	-0.551	2.077
β_1	effect of flood-proneness	-0.038	-0.272	0.194
β_2	effect of prior colony growth index	-0.409	-0.529	-0.287
β_3	effect of historical species richness	-0.093	-0.220	0.032
β_4	effect of historical abundance	-0.085	-0.153	-0.017
β_5	effect of presence of other disturbances	-0.084	-0.236	0.066
β_6	effect of Double-crested Cormorant abundance	-0.070	-0.138	-0.002
β_7	effect of Double-crested Cormorant management	-0.318	-0.613	-0.015
σ	standard deviation of colony growth index	0.625	0.581	0.675
σ_{survey}	standard deviation of survey random effect	0.785	0.055	5.512
σ_{lake}	standard deviation of waterbody random effect	0.058	0.002	0.192
σ_{site}	standard deviation of site random effect	0.046	0.002	0.128

Table S7. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Black-crowned Night-Heron colony growth used to examine the hypothesis that colony growth index is related to number of visits made for Double-crested Cormorant management (model 3 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.374	-1.033	1.880
β_1	effect of flood-proneness	-0.049	-0.277	0.187
β_2	effect of prior colony growth index	-0.409	-0.529	-0.288
β_3	effect of historical species richness	-0.093	-0.219	0.032
β_4	effect of historical abundance	-0.084	-0.153	-0.016
β_5	effect of presence of other disturbances	-0.085	-0.240	0.066
β_6	effect of Double-crested Cormorant abundance	-0.073	-0.140	-0.005
β_7	effect of Double-crested Cormorant management	0.012	-0.575	0.592
β_8	effect of # management visits in year t	-0.033	-0.123	0.057
β_9	effect of # management visits in year $t - 1$	-0.036	-0.119	0.045
β_{10}	effect of # management visits in year $t - 2$	-0.029	-0.111	0.054
σ	standard deviation of colony growth index	0.625	0.581	0.674
σ_{survey}	standard deviation of survey random effect	0.889	0.055	6.118
σ_{lake}	standard deviation of waterbody random effect	0.060	0.002	0.194
σ_{site}	standard deviation of site random effect	0.052	0.004	0.149

Table S8. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Black-crowned Night-Heron colony growth used to examine the hypothesis that colony growth index is related to cormorant management via number of nests oiled and number of birds culled (model 4 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.341	-0.906	1.570
β_1	effect of flood-proneness	-0.023	-0.265	0.217
β_2	effect of prior colony growth index	-0.430	-0.550	-0.306
β_3	effect of historical species richness	-0.102	-0.230	0.025
β_4	effect of historical abundance	-0.085	-0.154	-0.017
β_5	effect of presence of other disturbances	-0.085	-0.243	0.074
β_6	effect of Double-crested Cormorant abundance	-0.064	-0.135	0.006
β_7	effect of # nests oiled in year t	0.011	-0.059	0.081
β_8	effect of # nests oiled in year $t - 1$	-0.116	-0.239	0.003
β_9	effect of # nests oiled in year $t - 2$	0.070	-0.056	0.177
β_{10}	effect of # birds culled in year t	-0.027	-0.168	0.113
β_{11}	effect of # birds culled in year $t - 1$	0.020	-0.119	0.161
β_{12}	effect of # birds culled in year $t - 2$	-0.069	-0.157	0.038
σ	standard deviation of colony growth index	0.622	0.577	0.672
σ_{survey}	standard deviation of survey random effect	0.713	0.046	5.467
σ_{lake}	standard deviation of waterbody random effect	0.059	0.002	0.189
σ_{site}	standard deviation of site random effect	0.055	0.003	0.153

Table S9. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Ring-billed Gull colony growth used to examine the hypothesis that colony growth index is related to Double-crested Cormorant abundance (model 1 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.227	-0.863	1.378
β_1	effect of flood-proneness	-0.015	-0.177	0.147
β_2	effect of prior colony growth index	-0.423	-0.487	-0.361
β_3	effect of historical species richness	-0.090	-0.155	-0.023
β_4	effect of historical abundance	-0.060	-0.103	-0.017
β_5	effect of presence of other disturbances	0.002	-0.099	0.103
β_6	effect of Double-crested Cormorant abundance	0.036	-0.001	0.075
σ	standard deviation of colony growth index	0.670	0.643	0.698
σ_{survey}	standard deviation of survey random effect	0.621	0.083	3.955
σ_{lake}	standard deviation of waterbody random effect	0.047	0.003	0.133
σ_{site}	standard deviation of site random effect	0.026	0.003	0.067

Table S10. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Ring-billed Gull colony growth used to examine the hypothesis that colony growth index is related to presence of Double-crested Cormorant management (model 2 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.085	-1.397	1.647
β_1	effect of flood-proneness	-0.020	-0.180	0.144
β_2	effect of prior colony growth index	-0.421	-0.483	-0.359
β_3	effect of historical species richness	-0.095	-0.159	-0.031
β_4	effect of historical abundance	-0.061	-0.104	-0.019
β_5	effect of presence of other disturbances	0.001	-0.101	0.105
β_6	effect of Double-crested Cormorant abundance	0.034	-0.004	0.072
β_7	effect of Double-crested Cormorant management	0.156	-0.113	0.427
σ	standard deviation of colony growth index	0.670	0.643	0.698
σ_{survey}	standard deviation of survey random effect	0.836	0.084	5.990
σ_{lake}	standard deviation of waterbody random effect	0.045	0.002	0.130
σ_{site}	standard deviation of site random effect	0.024	0.001	0.069

Table S11. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Ring-billed Gull colony growth used to examine the hypothesis that colony growth index is related to number of visits made for Double-crested Cormorant management (model 3 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.073	-1.046	1.215
β_1	effect of flood-proneness	-0.019	-0.182	0.143
β_2	effect of prior colony growth index	-0.421	-0.482	-0.358
β_3	effect of historical species richness	-0.094	-0.159	-0.030
β_4	effect of historical abundance	-0.060	-0.104	-0.017
β_5	effect of presence of other disturbances	0.000	-0.100	0.102
β_6	effect of Double-crested Cormorant abundance	0.032	-0.006	0.069
β_7	effect of Double-crested Cormorant management	0.163	-0.300	0.630
β_8	effect of # management visits in year t	0.017	-0.023	0.058
β_9	effect of # management visits in year $t - 1$	-0.015	-0.063	0.034
β_{10}	effect of # management visits in year $t - 2$	0.002	-0.048	0.052
σ	standard deviation of colony growth index	0.671	0.645	0.699
σ_{survey}	standard deviation of survey random effect	0.605	0.081	3.291
σ_{lake}	standard deviation of waterbody random effect	0.045	0.002	0.124
σ_{site}	standard deviation of site random effect	0.027	0.001	0.068

Table S12. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Ring-billed Gull colony growth used to examine the hypothesis that colony growth index is related to cormorant management via number of nests oiled and number of birds culled (model 4 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.241	-1.466	1.910
β_1	effect of flood-proneness	-0.030	-0.191	0.136
β_2	effect of prior colony growth index	-0.421	-0.485	-0.356
β_3	effect of historical species richness	-0.091	-0.155	-0.027
β_4	effect of historical abundance	-0.061	-0.108	-0.016
β_5	effect of presence of other disturbances	-0.002	-0.104	0.100
β_6	effect of Double-crested Cormorant abundance	0.037	-0.002	0.076
β_7	effect of # nests oiled in year t	-0.015	-0.051	0.022
β_8	effect of # nests oiled in year $t - 1$	0.034	-0.021	0.094
β_9	effect of # nests oiled in year $t - 2$	-0.034	-0.113	0.034
β_{10}	effect of # birds culled in year t	-0.030	-0.097	0.032
β_{11}	effect of # birds culled in year $t - 1$	0.035	-0.031	0.102
β_{12}	effect of # birds culled in year $t - 2$	0.003	-0.056	0.066
σ	standard deviation of colony growth index	0.671	0.644	0.698
σ_{survey}	standard deviation of survey random effect	1.067	0.082	8.875
σ_{lake}	standard deviation of waterbody random effect	0.046	0.002	0.130
σ_{site}	standard deviation of site random effect	0.029	0.004	0.072

Table S13. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Herring Gull colony growth used to examine the hypothesis that colony growth index is related to Double-crested Cormorant abundance (model 1 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.094	-1.742	1.928
β_1	effect of flood-proneness	0.048	-0.030	0.127
β_2	effect of prior colony growth index	-0.329	-0.361	-0.296
β_3	effect of historical species richness	-0.017	-0.042	0.007
β_4	effect of historical abundance	-0.073	-0.095	-0.050
β_5	effect of presence of other disturbances	-0.002	-0.073	0.071
β_6	effect of Double-crested Cormorant abundance	0.042	0.024	0.062
σ	standard deviation of colony growth index	0.647	0.633	0.660
σ_{survey}	standard deviation of survey random effect	1.114	0.150	6.533
σ_{lake}	standard deviation of waterbody random effect	0.108	0.053	0.209

Table S14. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Herring Gull colony growth used to examine the hypothesis that colony growth index is related to presence of Double-crested Cormorant management (model 2 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	-0.386	-2.301	1.494
β_1	effect of flood-proneness	0.046	-0.031	0.125
β_2	effect of prior colony growth index	-0.330	-0.362	-0.298
β_3	effect of historical species richness	-0.024	-0.049	0.000
β_4	effect of historical abundance	-0.073	-0.096	-0.051
β_5	effect of presence of other disturbances	-0.007	-0.079	0.064
β_6	effect of Double-crested Cormorant abundance	0.037	0.018	0.056
β_7	effect of Double-crested Cormorant management	0.467	0.252	0.683
σ	standard deviation of colony growth index	0.645	0.632	0.659
σ_{survey}	standard deviation of survey random effect	1.095	0.159	5.863
σ_{lake}	standard deviation of waterbody random effect	0.105	0.049	0.210

Table S15. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Herring Gull colony growth used to examine the hypothesis that colony growth index is related to number of visits made for Double-crested Cormorant management (model 3 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	-0.493	-3.253	2.516
β_1	effect of flood-proneness	0.045	-0.032	0.122
β_2	effect of prior colony growth index	-0.330	-0.361	-0.299
β_3	effect of historical species richness	-0.024	-0.049	0.000
β_4	effect of historical abundance	-0.074	-0.097	-0.051
β_5	effect of presence of other disturbances	-0.007	-0.078	0.065
β_6	effect of Double-crested Cormorant abundance	0.037	0.018	0.057
β_7	effect of Double-crested Cormorant management	0.587	0.195	0.981
β_8	effect of # management visits in year t	-0.004	-0.025	0.018
β_9	effect of # management visits in year $t - 1$	-0.008	-0.035	0.020
β_{10}	effect of # management visits in year $t - 2$	-0.001	-0.029	0.025
σ	standard deviation of colony growth index	0.646	0.632	0.659
σ_{survey}	standard deviation of survey random effect	1.566	0.158	13.187
σ_{lake}	standard deviation of waterbody random effect	0.105	0.050	0.209

Table S16. Estimated means and 0.025 and 0.975 quantiles of posterior distributions of parameters estimated in the model of Herring Gull colony growth used to examine the hypothesis that colony growth index is related to cormorant management via number of nests oiled and number of birds culled (model 4 in “Supplemental Information: Model Specification”).

Parameter	Interpretation	Mean	0.025 Quantile	0.975 Quantile
β_0	intercept	0.079	-2.798	2.771
β_1	effect of flood-proneness	0.047	-0.029	0.124
β_2	effect of prior colony growth index	-0.329	-0.361	-0.297
β_3	effect of historical species richness	-0.018	-0.043	0.006
β_4	effect of historical abundance	-0.073	-0.096	-0.050
β_5	effect of presence of other disturbances	0.001	-0.070	0.073
β_6	effect of Double-crested Cormorant abundance	0.036	0.017	0.055
β_7	effect of # nests oiled in year t	0.002	-0.018	0.022
β_8	effect of # nests oiled in year $t - 1$	0.028	0.004	0.051
β_9	effect of # nests oiled in year $t - 2$	-0.010	-0.034	0.013
β_{10}	effect of # birds culled in year t	0.000	-0.041	0.041
β_{11}	effect of # birds culled in year $t - 1$	0.002	-0.040	0.044
β_{12}	effect of # birds culled in year $t - 2$	0.001	-0.019	0.022
σ	standard deviation of colony growth index	0.646	0.633	0.660
σ_{survey}	standard deviation of survey random effect	1.623	0.157	11.981
σ_{lake}	standard deviation of waterbody random effect	0.107	0.051	0.212