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Research Article

Great Lakes Double-Crested Cormorant Management Affects Co-Nester Colony Growth

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ABSTRACT The population of double-crested cormorants (*Phalacorocorax auritus*; cormorants) in the North American Great Lakes has increased substantially since the 1970s, sparking economic, social, and biological concerns that have led to widespread management of the species within United States waters. Previous studies have quantified behavioral impacts of cormorants on other waterbird species that share breeding colony sites with cormorants. However, no study has yet examined how these impacts might scale to entire colonies, nor have potential effects of cormorant management on co-nesters been examined. Our objective was to estimate effects of cormorant abundance and management on colony growth indices of 4 species that commonly co-nest with cormorants in the North American Great Lakes; 3 of these species are conservation or stewardship priorities for the region. We estimated colony growth using the Great Lakes Colonial Waterbird Survey and comparable Canadian surveys, conducted between 1976 and 2010. We then applied linear mixed models to determine association of co-nester colony growth indices with cormorant abundance and management presence and intensity while controlling for other factors that likely influenced growth rates. According to the fitted models, black-crowned night-heron (*Nycticorax nycticorax*) colony growth was negatively related to cormorant abundance and management, whereas great blue herons (*Ardea herodias*) had little response to cormorant abundance, and herring gulls (*Larus argentatus*) and ring-billed gulls (*Larus delawarensis*) responded positively to cormorant abundance and management. These results suggest that cormorant management may not be as neutral to co-nesters as is often assumed. Responsible management plans for cormorants should take into account the likely effects on co-nesters present so that conservation and management goals for co-nesters can also be met. © 2017 The Wildlife Society.

KEY WORDS *Ardea herodias*, culling, double-crested cormorant, *Larus argentatus*, *Larus delawarensis*, North American Great Lakes, *Nycticorax nycticorax*, *Phalacrocorax auritus*, population growth.

The population of double-crested cormorants (*Phalacrocorax auritus*; cormorants) in the North American Great Lakes has increased substantially since the 1970s, largely because of protection from persecution and bans on organochlorine pesticides (Weseloh et al. 1995). Across the 5 Great Lakes and their connecting waterways, results of surveys in the United States and Canada reported only 598 nesting pairs of cormorants in 1977; in 2007, 97,188 nesting pairs were recorded (Wyman et al. 2016). Cormorant population growth was initially seen as a conservation success story, but as growth continued, attitudes towards cormorants 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 cormorants (Weseloh et al. 2002, Wires 2014).

In 2003, the United States Fish and Wildlife Service (USFWS) established a Public Resource Depredation Order (50 CFR 21.48), enabling cormorant colonies in United States Great Lakes states to be managed to reduce colony sizes. By 2007, a majority of cormorant colony sites in the United States Great Lakes had been subject to some form of management (Wires and Cuthbert 2010). Management of cormorant colonies in Canadian Great Lakes began in 2004 but was limited to only a few sites (Wires 2014). The 2 primary methods of management used in the United States were spraying eggs with food-grade corn oil so that embryos asphyxiate, and culling adult birds at breeding colonies

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during the nesting season (Blokpoel and Hamilton 1989, Wires 2014). Less frequently, birds were culled or harassed outside the breeding season or nests were destroyed (Dorr et al. 2012, Farquhar et al. 2012).

Cormorants rarely nest alone in the Great Lakes (Wires and Cuthbert 2010, Wyman et al. 2016), so cormorant abundance and cormorant 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 or did not conclusively link declines directly or indirectly to activities of cormorants (Skagen et al. 2001, Cuthbert et al. 2002). On the other hand, cormorant 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, cormorants 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 cormorant management have received little direct research attention. Cormorants, however, exhibit increased interspecific aggression as a result of human disturbance (Drapeau et al. 1984), which is important because most management operations require humans to enter the breeding colony (T. J. Doyle, USFWS, 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 effects of cormorants and their management is important for designing responsible management plans.

The goal of our study was to quantify potential effects of cormorant 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 cormorants 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: co-nester colony growth is related to cormorant abundance, co-nester colony growth is related to the presence or absence of cormorant management, co-nester colony growth is related to the intensity of cormorant management, and effects of cormorant management differ according to the type of management (i.e., nest oiling, 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, 1998; Scharf and Shugart 1998; Cuthbert et al. 2010; Cuthbert and Wires 2013), from which we obtained United States waterbird colony data, included United States waters of the 5 Great Lakes (Ontario, Erie, Huron, Michigan, Superior) and their connecting waterways (i.e., St. Lawrence, Niagara, Detroit, and St. Marys rivers, and Lake St. Clair). The study area also included the coastline up to 1 km inland between Massena, New York, USA, and Pigeon Point, Minnesota, USA. The eastern boundary of the study area was extended to Massena, New York 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 (i.e., Ontario, Erie, Huron, Superior) and Canadian waters of the St. Lawrence, Niagara, and Detroit rivers. Colonies located along the mainland coastline between Cornwall, Ontario, Canada and the United States-Canadian border at the west end of Lake Superior were also included (Morris et al. 2003).

The North American Great Lakes proper cover an area of over 240,000 km^2 (The Nature Conservancy Great Lakes Program 1994) and contain nearly 32,000 islands (Vigmostad et al. 2007). Topography is variable across the region: Lake Superior features rugged, rocky shorelines, with bedrock cliffs reaching up to 80 m above the lake surface, whereas the shores of Lake Erie tend to have low relief, with large sand spits and abundant coastal wetlands (Larson and Schaetzl 2001, Albert 2003). The wintertime climate is characterized by Arctic air masses and frequent storms, while the summer season brings heat, humidity, and thunderstorms (Hayhoe et al. 2010). Summer is the wettest season, and also the time when lake levels reach their annual peak (Keough et al. 1999, Hayhoe et al. 2010). Changes in precipitation and evaporation rates can result in interannual lake level fluctuations of up to 2.5 m (Albert 2003). Each of the 5 Great Lakes possesses a unique combination of physical characteristics (i.e., temperature, alkalinity, salinity, phosphorus availability, and turbidity). These characteristics in turn influence the plant communities found on the shores and islands of each of the lakes (Keough et al. 1999). Vigmostad et al. (2007) provide a thorough summary of the biotic features of Great Lakes islands. The dominant land use types in the United States Great Lakes basin are forest and agriculture, with developed land area growing fastest in coastal areas (Wolter et al. 2006). On the Canadian side of the border, agricultural and developed land uses decline and forest land use increases with increasing latitude (Lougheed et al. 2001).

METHODS

Waterbird Colony Data

The GLCWS in the United States (Scharf 1978, 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) described 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. Census techniques included ground counts of marked nests, counts made from boats, and counts made from aerial photographs;

the census method of choice depended on the size and structure of the colony and the accessibility of the colony site. Nests were included in the colony count if they contained eggs or chicks or showed other signs of active use. Four surveys were conducted in the United States and Canada during 1976–2010: 1976–1980, 1989–1991, 1997–2000, and 2007–2010 (Morris et al. 2003, Cuthbert and Wires 2013). Field methods followed standard ethical practices for observational studies of wild birds (Fair et al. 2010).

We use the term colony to describe a group of individuals of a single species nesting at a site, rather than all individuals (of various species) 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 followed Guillaumet et al. (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, and $\max(N_s, N_{s-1})$ indicates that the larger of the values N_s and N_{s-1} should be used here. With this definition, 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, and values between 0 and 1 indicate increasing nest abundance. We assigned sites that were unoccupied from one survey to the next an index value of 0 to indicate no change. Guillaumet et al. (2014) referred to this calculation as growth rate; we prefer growth index because we measured colony growth over time periods that varied slightly in length according to when surveys were completed.

Model Covariates

Many intrinsic and extrinsic variables may influence the occupancy and abundance dynamics of colonial waterbirds. We were primarily interested in covariates related to cormorant abundance and cormorant management. We obtained data on cormorant abundance from the GLCWS and Canadian surveys (Cuthbert and Wires 2013; D. J. Moore, personal communication). We obtained data on cormorant management in the United States from the USFWS; data included information on locations, dates, numbers of cormorant eggs oiled, numbers of nests destroyed, and numbers of cormorants 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 cormorants 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. To determine the effect of cormorant management presence on co-nester colony growth index, we included a covariate indicating whether cormorant management had been applied at the colony site since the preceding survey.

We measured management intensity in 2 ways: how many visits were made to perform management activities, and how many cormorants were affected by management in terms of nests oiled and adults culled. To determine the effect of increasing management intensity in the form of number of management-related visits to the site, we added covariates for numbers of management-related site visits in the survey year and the preceding 2 years (3 covariates), in addition to presence-absence of management. To determine the effect of increasing management intensity in the form of number of cormorants affected, we included covariates for numbers of nests oiled and numbers of cormorants culled in the survey year and the preceding 2 years (6 covariates). If management in the survey year occurred after the colony census, management covariates for that year equaled 0.

We controlled for the influence of 5 additional variables in modeling the relationship between colony growth index and cormorant abundance and management: historical nest abundance, historical species richness, colony site flood potential, historical colony growth index, and presence of other sources of disturbance at the colony site. Wyman et al. (2014) previously identified historical nest abundance, historical species richness, and flood potential of a colony site as significant influences on occupancy dynamics of colonial waterbirds in the Great Lakes. 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 we calculated the response variable, colony growth index. We obtained values for flood potential primarily from GLCWS data, with expert opinion filling in gaps in GLCWS observers' records. We considered a site 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. We determined flood potential 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 cormorants 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. We calculated the colony growth index as described above for the response variable.

Because one of the ways in which cormorant 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 cormorant 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 waterbird colonies in the Great Lakes have a 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, NY, 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; we coded locations named in these publications 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 cormorant abundance and management, along with nuisance covariates, to co-nester colony growth index values. For each species, we fit 4 models (see Supporting Information, available online, for full model specifications in statistical notation). All models included historical nest abundance, historical species richness, flood potential, historical growth index, other disturbance, and cormorant 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 approximately 1,500 unique herring gull colony sites. Prior to model fitting, we scaled all numerical covariates 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). We constructed distributions for missing data using means and standard deviations of observed data for the species in question. Mimicking empirical distributions as much as possible, we modeled historical species richness, number of management visits, number of nests oiled, and number of adults culled with normal distributions truncated at 0; historical abundance and cormorant abundance with exponential distributions; flood potential with a Bernoulli distribution; and prior colony growth index 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 Monte Carlo standard error <2% of posterior distribution standard deviation, and $\widehat{R}$ statistics (Gelman and Rubin 1992) of <1.1 for all parameters. In addition to $\widehat{R}$, we monitored convergence by visual inspection of trace plots. We discarded a burn-in period of 2,000 iterations and thinned chains by 10 because of 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

Since 1976, cormorant colonies have been recorded on all 5 of the North American Great Lakes and in the connecting waterways. Cormorant management activities have also occurred broadly across the United States waters of the Great Lakes (Fig. 1). Four common co-nesters of cormorants shared colony sites with cormorants in 12–43% of occurrences in the North American Great Lakes between 1976 and 2010 (Table 1). Between 1% and 7% of co-nesting occurrences also occurred in the presence of cormorant management (Table 1). When considering the survey from 2007 to 2010 alone, 4–16% of co-nesters' colony sites were subject to cormorant management.

Cormorant abundance was associated with co-nester colony growth index for all species except great blue herons, but the direction of association varied (Fig. 2). Cormorant abundance was associated with a lower or more negative colony growth index for black-crowned night-herons, whereas cormorant 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 online in Supporting Information).

The presence of management was associated with a strongly increased colony growth index for herring gulls (Fig. 2). 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. 2). As with cormorant abundance, responses of great blue heron colony growth index values to the presence of cormorant management were neither predominantly positive nor predominantly negative (Fig. 2).

In the year prior to survey, more management visits were weakly associated with a reduced colony growth index for all species (Fig. 3; Tables S3, S7, S11, and S15). For black-crowned night-herons, this association held for the current year and 2 years previously (Fig. 3; 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. 3, Table S7). For all other species, the presence of management had an effect beyond the number of visits; presence of management changed the slope of the relationship between

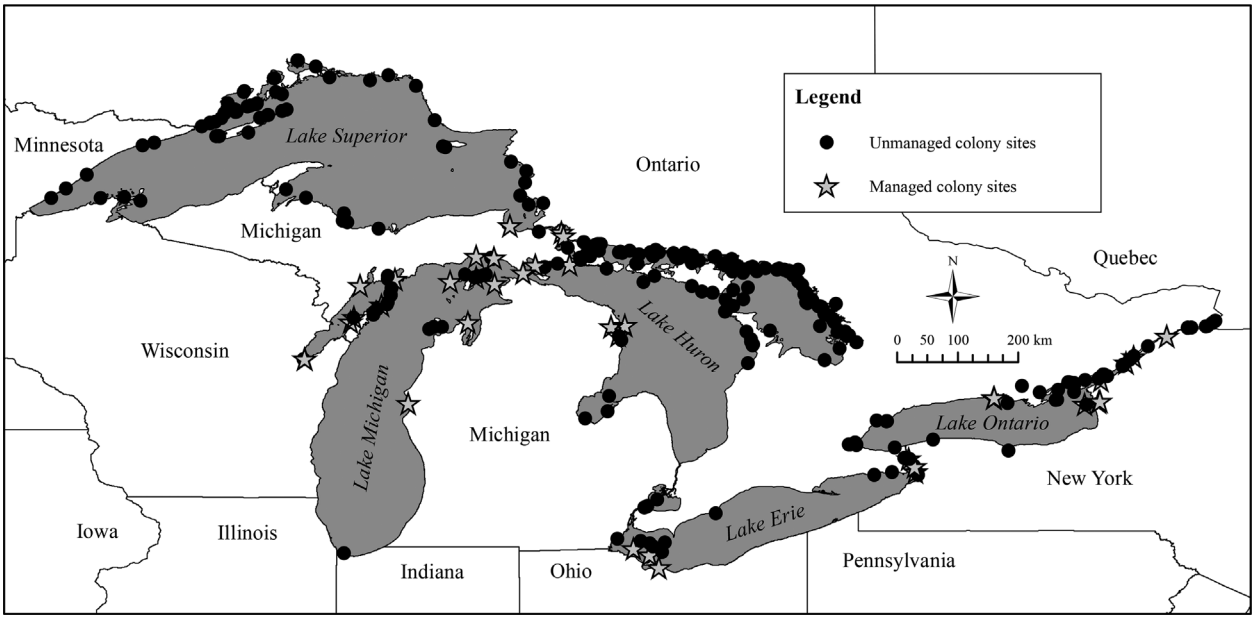

Figure 1. Double-crested cormorant colony sites in the North American Great Lakes, 1976–2010, as identified by the Great Lakes Colonial Waterbird Survey (Cuthbert and Wires 2013) and comparable surveys in Canada (D.J. Moore, personal communication).

number of visits and colony growth index for visit numbers >0 (Fig. 3).

Effects on co-nesters often differed according to the management method used (Fig. 3; 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 clear association with number of cormorants culled, and mixed responses to number of nests oiled depending on the lag time between management and survey (Fig. 3, 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 culling and nest oiling in the survey year (Fig. 3). 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 well, 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 cormorants and their management.

DISCUSSION

The 4 colonial waterbird species that most commonly co-nest with cormorants in the Great Lakes showed variable responses to cormorant presence and management. These results suggest that the prevailing assumption that cormorant management can only be neutral or beneficial to co-nesting waterbird populations (USFWS 2014) is incorrect. 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 Cormorant Abundance and Management

Herring gulls and ring-billed gulls showed a strongly positive response to cormorant abundance, contrary to an earlier finding by Somers et al. (2007) of reduced reproductive success in herring gulls nesting with cormorants. The herring gull work conducted by Somers et al. (2007, 2011) may have

Table 1. Distribution of double-crested cormorants (cormorants) and cormorant 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
No. colony occurrences	330	224	768	3,780
No. colony occurrences with cormorants present	77	97	179	448
No. colony occurrences with cormorant management	10	15	18	36
No. observations used to fit models[a]	501	390	1,299	4,761

[a] Number of observations used to fit models includes 3 observations (taken in 1989–1991, 1997–1999, and 2007–2010) from all sites occupied by the co-nesting species at least once within the 4 survey periods.

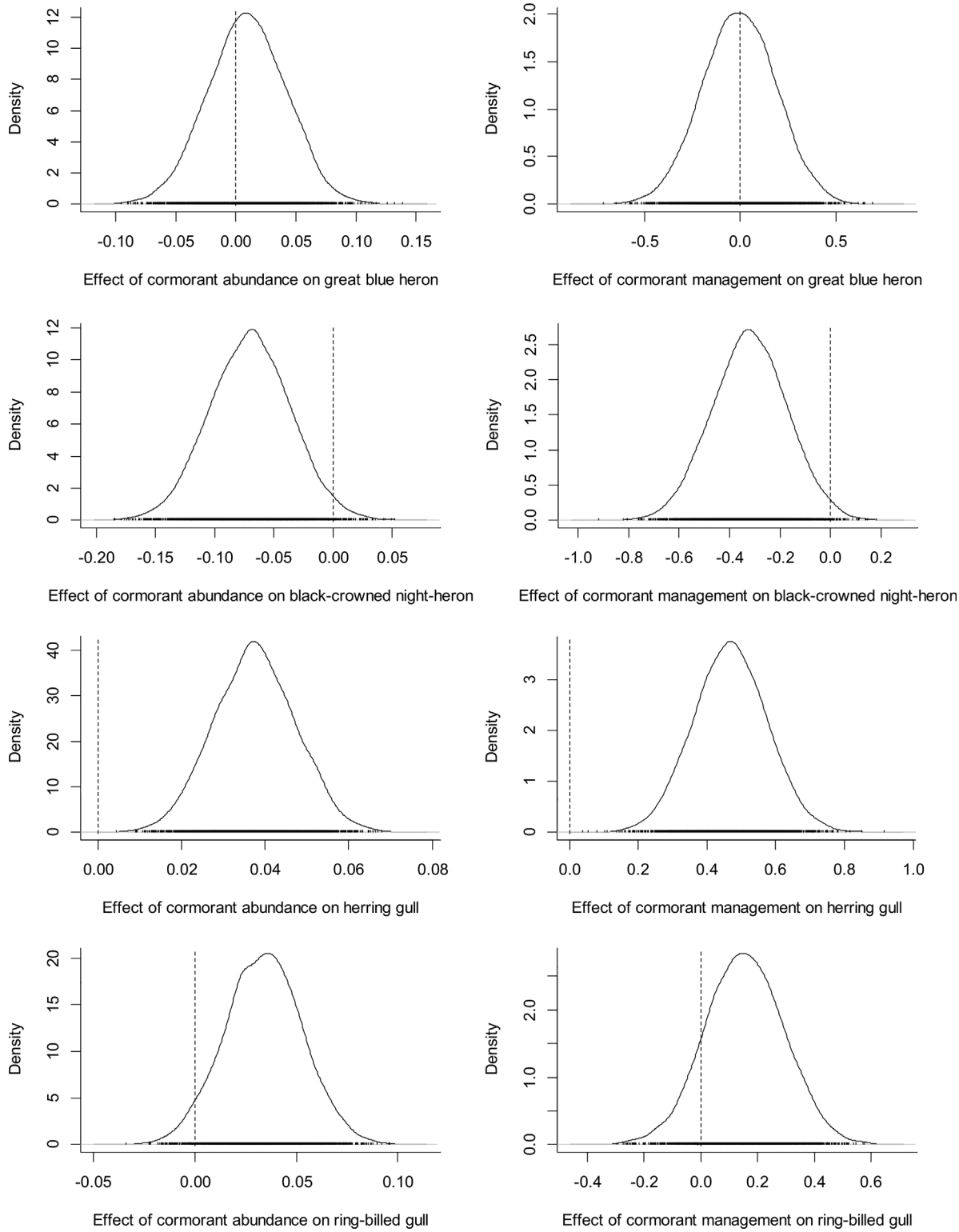

Figure 2. Estimated posterior densities for effects of double-crested cormorant (cormorant) abundance and presence of management on colony growth index for 4 colonial waterbird species that nest with cormorants in the North American Great Lakes, 1976–2010. Dotted lines show the location of 0, the value indicating no effect. Note the variation in scale of the *x*-axis among plots. Cormorant abundance was scaled to have a standard deviation of 1 prior to model fitting.

been confounded by human disturbance, but according to our fitted models, herring gulls in particular have an almost exclusively positive response to presence of cormorant management, a situation in which human disturbance is almost unavoidable. Indeed, there are indications that cormorant management is associated with increased herring gull nest success (B. S. Dorr, U.S. Department of Agriculture [USDA] Wildlife Services, personal communication).

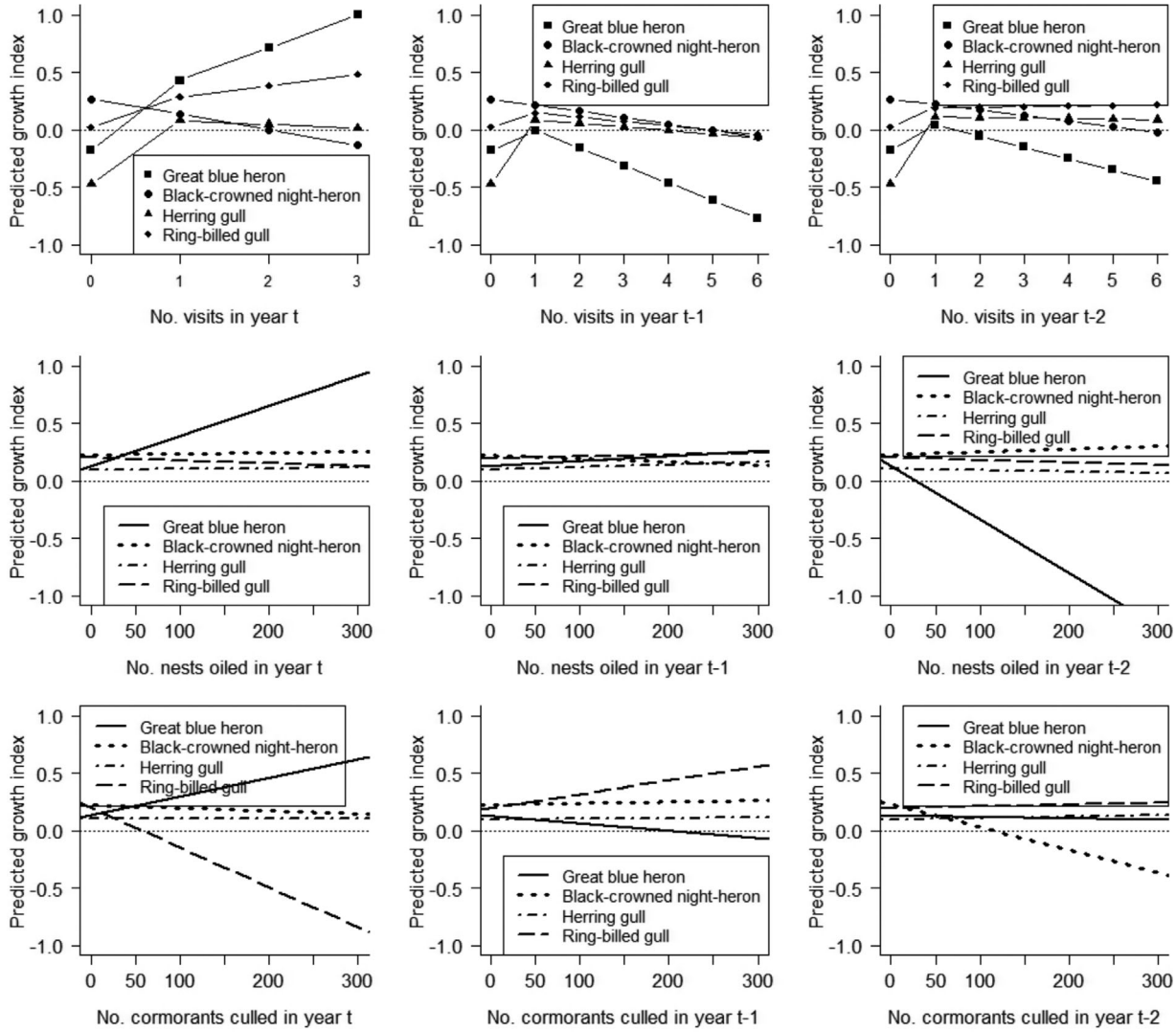

Figure 3. Mean predicted colony growth index of 4 waterbird species in the North American Great Lakes, as a function of number of double-crested cormorant (cormorant) management visits (top), number of cormorant nests oiled (middle), and number of cormorants culled (bottom) in the year of survey and the 2 previous years. Colony growth index values range from −1 to 1, and were calculated for each interval between decadal surveys conducted from 1976 through 2010. Effect of presence or absence of cormorant management is included in predicted colony growth index value as a function of number of visits; we added an effect of management presence if number of visits was >0. All other covariates were held constant at their median, except for cormorant abundance, which was held constant at the median value for sites with double-crested cormorants present.

Several researchers have reported 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 reported to affect as much as 95–100% of cormorant nests, depending on gull colony size and location, where cormorants were nesting, and timing of disturbance, among other factors (F.J. Cuthbert, University of Minnesota, personal observation; N. E. Seefelt, Central Michigan University, personal communication). Gull depredation of cormorant 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 undermine 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. 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), whereas herring gulls are typically ground-nesters and ground-foragers (Pierotti and Good 1994). Herring gulls did show a positive response to egg-oiling in the year prior to survey, 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 cormorant nest may decline as more nests are available for depredation.

Black-Crowned Night-Heron Response to Cormorant Abundance and Management

Both cormorant presence and cormorant management reduced black-crowned night-heron colony growth index, with more management visits associated with greater reductions. Cuthbert et al. (2002) similarly reported an association between black-crowned night-heron declines at colony sites and cormorant presence but observed no direct interactions between black-crowned night-herons and cormorants 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 effect of cormorants on nest site vegetation is a potential alternative mechanism for how cormorant abundance affects black-crowned night-heron colony growth index. Higher cormorant 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). In the Great Lakes, black-crowned night-herons nest almost exclusively in dense sub-canopy trees, shrubs, and grasses (Cuthbert and Wires 2013), so reductions in understory vegetation can lead to declines in black-crowned night-heron nest abundance (Shieldcastle and Martin 1997).

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). Cormorants are not the only threat to the species, and indeed, closer examination of individual colony site histories led Cuthbert et al. (2002) to conclude that factors other than cormorants were responsible for black-crowned night-heron declines at several Great Lakes colony sites. Alleviation of cormorant effects on black-crowned night-herons has been invoked as a reason for cormorant management and a dataset on cormorant management effects 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 cormorant management (Wires et al. 2011, Thorndyke and Dobbie 2013). Our results showed that although positive responses to cormorant management may occur, negative responses are likely to be much more common. 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 cormorants affected by management. This contrast suggests that disturbance may be the most problematic part of cormorant 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 Cormorant Abundance and Management

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

Great blue heron mean responses to management activity were quite variable, 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. Culling is the predominant management approach for tree-nesting cormorant colonies. Removal of tree-nesting cormorants 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 1,000 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 because 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

The Public Resource Depredation Order is no longer in effect, and management of cormorants in the United States Great Lakes has been reduced since 2015, the last year that management occurred under the Order. However, cormorant management is likely to continue at selected sites under depredation permits. A responsible management strategy for cormorants needs to take into account the co-nesting species that may be affected by management activities, including how those species typically respond to cormorant management and what conservation or management concerns exist for the co-nesting species themselves. If cormorant management is deemed desirable, management at shared colony sites may best be conducted at night, when gulls are unlikely to depredate unattended cormorant nests (Duerr et al. 2007) and benefit from cormorant management. This will also help prevent gulls from undermining the goal of cormorant management and keep cormorants from abandoning oiled nests.

Where cormorant 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 cormorant abundance and to increasing numbers of visits for cormorant management purposes. However, there are local exceptions where cormorant management has resulted in increased black-crowned night-heron abundance (Farquhar et al. 2012). Managers should carefully consider whether cormorant management is 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 cormorants (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 cormorants nest abundantly. Such a strategy would help minimize conflict between the 2 species and reduce use of cormorant management at black-crowned night-heron colony sites.

In a community as diverse as that of colonial waterbirds breeding in the North American Great Lakes, it is not surprising that dramatic population growth or intensive management of one member of the community would have effects on other members of the community. As this study of the North American Great Lakes has shown, managers would do well to consider potential effects of management and the target species for management on other community members when designing and implementing a management program.

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