

METHODS FOR REFINING WATERBIRD COLONY PERSISTENCE RESEARCH  
AND THEIR APPLICATION TO GREAT LAKES COLONIAL WATERBIRDS

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## **DEDICATION**

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## ABSTRACT

After decades of research on waterbird colony persistence, or the re-occupation of a colony site in successive breeding seasons, many environmental correlates of colony persistence have been identified. However, little is understood about what truly drives waterbird colony persistence at a given site; without identifying causative factors, a full understanding of the form and function of colony site use patterns is impossible. To improve understanding of the biology of colonial waterbirds as well as conservation and management efficiency, greater research attention should be directed towards multivariate analyses of predictors of colony persistence and towards experimentation to test theoretical predictions about mechanisms determining colony site use. The former type of research allows scientists to identify the most important variables among a suite of potential predictors, while the latter is the only legitimate way to determine true causative relationships. A series of decadal surveys of Great Lakes waterbird colonies provides an opportunity to illustrate the method of multivariate analysis to inform biological and conservation understanding. I used a hierarchical occupancy model analyzed within a Bayesian statistical framework to determine the most important predictors of site colonization and colony persistence probabilities for the ten most common species in the U.S. Great Lakes colonial waterbird community. Species varied considerably in their responses to site location, human disturbance, and species richness at colony sites. Sites with large colonies and those not susceptible to flooding were most likely to be reoccupied in the following census period, suggesting that sites with these characteristics should be conservation priorities. However, the most effective

conservation strategy will take advantage of knowledge about species-level variation to tailor conservation and management activities to the particular species of interest.

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## PREFACE

Large waterbird breeding colonies are salient features of coastal and lacustrine landscapes, with birds fanning out across the sky as they travel between their nests and feeding grounds. In some places, people anticipate the arrival of birds to a traditional colony site each spring as the weather begins to warm. In other places, colonies assemble and disband from year to year or even within a single season. The length of time and the regularity with which waterbird colonies occupy certain sites has important implications for the birds that nest there. Long-term site occupancy allows for adaptation to the site environment, for example by selection for an egg color that matches the nesting substrate (Sánchez et al. 2004). However, new colonies can play an important role in population dynamics, as evidenced by higher annual growth rates (Creutz 1967, Hénaux et al. 2007) and greater productivity (Tims et al. 2004).

Patterns of site use by breeding colonial waterbirds have consequences for conservation and management as well. Understanding the most important causative factors affecting colony site use can increase efficiency of colonial waterbird conservation and management. Given the pressure for waterfront development and the limited resources available to environmental agencies and organizations, it is generally not possible to protect and manage all potential colony sites for a waterbird population that changes breeding locations over time. Ability to predict the likelihood of a colony's return to a breeding site in future years reduces the risk associated with conservation and management activities because emphasis can be placed on highly persistent colonies

where actions like conservation easements and vegetation management have a more certain payback.

In the following chapters, I demonstrate that colony persistence research needs to move beyond simple correlative studies to better identify drivers behind patterns of colony persistence. In the first chapter, I suggest that multivariate modeling and experimentation will help waterbird scientists come closer to an understanding of why certain colony locations are more stable than others. In the second chapter, I apply the technique of multivariate modeling to colony persistence in Great Lakes colonial waterbirds, identifying the most important predictors of colony site use patterns and illustrating their relevance for regional colonial waterbird conservation and management.

**CHAPTER 1:**  
**USING MULTIVARIATE MODELING AND EXPERIMENTAL TECHNIQUES**  
**TO UNDERSTAND COLONY PERSISTENCE**

Colonial waterbirds congregate each spring to form breeding colonies in which they may benefit from shared information on resource availability and communal defense against predators (Burger 1981). Patterns of site use across breeding seasons provide insights into the biology of this group of birds, including the relative influences of resource availability and social dynamics on their nesting decisions and how they react to changes in their environment. After decades of research on colony persistence, the re-occupation of a colony site in successive breeding seasons, many correlates of colony persistence have been identified. However, little is currently known about what truly drives waterbird colony persistence at a given site. Without identifying causative factors, a full understanding of the form and function of colony site use patterns is impossible.

The accepted approach for answering any question of causation in science is to perform experiments exhibiting randomization, replication, and control. Experimental manipulation of colony site dynamics is not often feasible, given the large spatial scale on which this process operates and the complexity of controlling confounding factors within a natural environment. The present study reviews the existing body of research on potential predictors of colony persistence and explores ways to address the question of causation while acknowledging the inherent challenges. Where experimentation is impossible, I suggest expanding the use of multivariate modeling techniques to determine

the relative importance of different variables in regulating colony site dynamics. Focusing on variables with the strongest connections to site use will more closely approximate causation than will continuing to conduct single-variable analyses involving each potential predictor of colony persistence. On the other hand, by breaking down observations and theories about colony site dynamics into simple predictions, some of these observations and theories become testable through experimentation. As illustration, I provide examples of how straightforward experiments could be applied to a belated critical evaluation of untested theories about colony site dynamics. The caveat to these suggested research directions is that the literature has frequently demonstrated variation in colony persistence patterns by both species and region, and indeed there may be no single theory of causation that proves true across the board. At present, *in situ* research remains the most accurate way to inform future conservation and management of colonial waterbirds, and to the extent that identification of causal factors is possible, conservation and management activities based on causal relationships are those most likely to succeed.

## LITERATURE REVIEW

I reviewed the existing literature to understand the types of scientific studies that have examined the relationship between waterbird colony persistence and environmental variables and to summarize their major findings. To identify such studies, I completed subject-based searches within the internet subscription databases Web of Science, Wildlife and Ecology Studies Worldwide, and Zoological Record. I performed similar searches in JSTOR, ScienceDirect and BioOne to account for particularly old or new



research that may not have been included in the other databases. I also used the citation-based searching capability of Web of Science to examine papers cited by or citing identified articles. Subject-based searches used a set of synonyms for “colony” combined with a set of synonyms for “persistence” (Table 1), which were then combined with common and scientific species names or family names to limit results to taxa of interest. Families of interest included Pelecanidae (pelicans), Phalacrocoracidae (cormorants), Anhingidae (anhingas), Ardeidae (herons and egrets), Threskiornithidae (ibises), Ciconiidae (storks), Phoenicopteridae (flamingos), and Laridae (gulls, terns, and skimmers). I also included one study on the Common Eider (*Somateria mollissima*) that appeared in the course of conducting the described searches. I excluded families and species of colonially breeding waterbirds with oceanic colony sites, due to the major differences between that environment and the environment of mainland and near-shore island colonies. Other criteria for selected papers included that the study must consider persistence or abandonment of colonies (i.e., papers that examined only the colonization aspect of site occupancy dynamics were excluded), and that its conclusions must be based on data collected from three or more breeding sites in multiple years.

I identified 42 articles that examined potential predictors of colony persistence and fit all specified criteria (Appendix 1). These papers were published in 16 different journals, although nearly half were published in *Waterbirds* and its predecessors (*Colonial Waterbirds* and *Proceedings of the Colonial Waterbird Group*). The articles examined the colony site dynamics of 50 different species in 29 U.S. states and 11 other countries, although none of the studies were sited in Africa, Asia, Australia or Oceania.

The most commonly studied species has been the Wood Stork (*Mycteria americana*); its site use dynamics were reported in ten different studies. The median number of unique breeding periods included per study was 6.5, while the median number of sites included was 41. Only 25 articles used inferential statistics to support their conclusions and only six of these considered multiple predictors simultaneously in their analyses.

I categorized potential predictors of colony site dynamics from the 42 identified studies into 13 different groups (Table 2). The four variables most commonly examined as potential predictors of colony persistence were colony size, habitat change, habitat type, and species identity. Overall, the average study considered predictors in only two categories, although the six multivariate modeling studies included an average of more than three categories of predictors. Both univariate and multivariate studies strongly suggest that colony persistence is positively related to colony size, negatively related to the rate of habitat change, and varies according to species identity (Table 2). There is less consistent support for a relationship between colony persistence and habitat type. Finally, many potential predictors of colony persistence only appear in a handful of studies and deserve further research attention, such as human disturbance, availability of food resources, and the geographic location of colony sites, i.e., the effect of population identity.

More discussion of the findings of the literature review and their implications will occur as they become relevant in the following sections, but one result highlights the importance of studying colonies rather than individuals if the stated goal is an understanding of colony behavior. Although reproductive success is typically an

important determinant of individual site fidelity (Cuthbert 1988, Parejo et al. 2006, Vergara et al. 2006), only one of five colony persistence studies found colony-wide reproductive success to have a strong influence on colony persistence (Table 2). Colony persistence does not require that any of the individuals breeding at a site in one year return to the site in the following year, as long as some individuals of the same species do. Whatever site characteristics enticed birds to nest at a place where they experienced poor reproductive success may still be attracting new birds to the site even when the original breeders leave. Indeed, Southern and Southern (1982) demonstrated that when part of a former nesting habitat was bulldozed between breeding seasons, most birds previously nesting in the altered area moved to an undisturbed portion of the colony site while new breeders colonized the disturbed portion so that it remained occupied. In another study of unmarked birds, a colony site remained active through eight seasons of complete reproductive failure due to predation (Southern et al. 1985). Thus, in attempting to understand colony persistence, it is critical to focus directly on the behavior of colonies rather than attempting to scale up from prior knowledge about the behavior of individuals.

#### MULTIVARIATE MODELING TO ACHIEVE SYNTHESIS

The relationships between ecological variables and patterns of colony site use through time were studied exclusively through univariate correlational and modeling studies until the very end of the twentieth century (Erwin et al. 1998). More recently, modeling studies that include multiple simultaneous predictors have become important

for understanding ecological determinants of colony persistence, coincident with the development of various occupancy modeling techniques (Barbraud et al. 2003, MacKenzie et al. 2006, Royle and Dorazio 2008). Failure to take into account all relevant variables may lead to false inferences through Simpson's paradox (Simpson 1951), a situation in which the relationship between two variables changes direction when interaction with a third variable is considered. Although neither univariate nor multivariate modeling studies can determine causality, multivariate modeling studies may be able to discriminate among a suite of simultaneously considered predictors to highlight the most important correlates of variation in persistence patterns. For example, nearly all univariate studies and most multivariate studies find a positive relationship between the number of breeding pairs using a colony site and the likelihood that the colony site is occupied through multiple breeding seasons (Table 2). With a generalized linear mixed model containing seventeen explanatory variables, Martinez-Abraín and colleagues (2003) were able to distinguish among competing predictors and determine that changes in abundance are actually more important in predicting colony persistence than colony size itself.

As compared to univariate studies, multivariate modeling analyses have identified fewer factors overall that significantly influence colony persistence. Less than one-fifth of the studies using univariate analyses reported any non-significant factors, while half of all studies using multivariate analyses reported at least one non-influential factor. Several possible explanations exist for this discrepancy. As suggested above, the difference could result from the ability of multivariate analysis to reject factors that add little additional

information to the analysis when more influential factors are also included. Secondly, analyzing many relationships individually increases the chance of making a Type I statistical error, in which the null hypothesis (that the predictor has no effect on the response) is rejected but is actually true. None of the studies examined used procedures to control for Type I errors. If univariate studies do not correct for this problem, they may give the impression that more variables are influential than is actually the case. Thirdly, a modeler is expected to report all variables included in his or her most general model whether they end up being significant or not. Model selection is an important part of the methods of multivariate studies, and these studies typically describe the most general model and the process used to select the best model. In contrast, although “data dredging” to find significant relationships is frowned upon, there is no standard expectation that univariate studies report all relationships investigated. Thus, authors of univariate studies can choose not to report findings that are not significant as long as these findings do not bear strongly on their hypotheses. Scientists studying colony site dynamics as well as those in other scientific fields should be aware of this potential for bias in univariate studies and should seek to avoid it, not always an easy task given the perception that significant findings are more interesting and more worthy of publication.

Opportunities for improvement of multivariate modeling of colonial waterbird site dynamics remain. First, multivariate modeling studies could be strengthened by expanding their range of predictor variables to include all the variables supported in correlational studies. Multivariate modeling appears to be relatively slow to catch on among colony site dynamics researchers, with more correlational studies than

multivariate modeling studies published since the first multivariate modeling analysis by Erwin and colleagues (1998). For example, multivariate modeling studies have yet to examine either disturbance or geographic location (population identity) as determinants of colony persistence, both of which are supported by correlational studies (Table 2). Second, no multivariate modeling study has compared predicted occupancy to real occupancy data gathered from the same population as the data on which the model was built. Adding in this test would help to confirm or refute the conclusions of the original modeling study, thus bringing the results of multivariate modeling studies closer to what can be achieved through experimental manipulation.

#### TESTING THEORY

Experimental manipulation, the ideal of the scientific method, is notably absent from the colony persistence literature. Experimental research has been used with colonial waterbirds to answer other types of questions, such as the function of social attraction in colony site choice (Burger 1988) or nesting substrate preference (Quinn and Sirdevan 1998). However, none of the research reviewed for the present study includes experimentation with control, randomization, and replication. Field studies of colony persistence have tended to either take existing theories as fact or else avoid theoretical explanations for the patterns observed. The process of developing theories on colony persistence can lead to a deeper understanding of colony site use patterns, but without direct tests, biologists and wildlife managers cannot rely on theory to be an adequate reflection of reality and the theories' flaws cannot be identified and rectified.

There are few proposed theories that predict patterns of colony site use, and they can be divided into the habitat stability theory (McNicholl 1975) and colony size selection theories (Shields et al. 1988, Brown and Rannala 1995, Russell and Rosales 2010). McNicholl's theory on habitat stability (1975) is probably the most influential theoretical work on colony persistence. McNicholl posits that in stable environments, individuals should have high site fidelity, returning to the same sites year after year to breed. In unstable environments, individuals should show greater attachment to a familiar group of conspecifics than to a specific breeding site and should move with this group from site to site as conditions change (an idea first described by Austin (1951) as "group adherence"). Colony size selection theories, on the other hand, attempt to explain why not all colonies have the same number of breeding individuals. These theories are not primarily concerned with colony persistence, but their predictions sometimes relate to colony stability; such an indirect relationship probably explains the lack of reference to these theories by authors of field studies on colony persistence. Building on Fretwell and Lucas's "ideal free distribution" (1969), where the density of individuals at a location increases with increasing habitat quality, Shields and colleagues (1988) and Brown and Rannala (1995) suggest that large colonies provide social signals of habitat quality and thus will persist and remain large over time. A newer theory by Russell and Rosales (2010) states that potential colony sites that have large carrying capacities should be used frequently but that the number of consecutive seasons in which these sites are occupied depends on the ability of individuals to choose the most attractive colony site, with attractiveness determined by available nesting space and the number of conspecifics

already present. If individuals are very good at assessing and choosing colony sites, then a few large colony sites will be highly persistent, but when individuals cannot assess sites accurately, the locations of the large colonies fluctuate frequently. The above theories find some support when applied to observed patterns of site use (Brown and Rannala 1995, Russell and Rosales 2010), but no direct experimental testing has been conducted for any of the theories with regard to colonial waterbirds. Once these theories receive experimental support or falsification, they can help conservationists and managers predict future site use by colonial waterbirds and manipulate site use if necessary to achieve conservation objectives.

Experiments on colony occupancy must overcome two major barriers: the huge spatial scale at which colony site dynamics operate and the complexity of controlling for all sources of natural variability between colony sites. One option to address the first problem is to use spatially segregated subcolonies within a colony as a model for colonies within a population, with the assumption that relationships scale evenly (subcolony persistence patterns often mirror the patterns observed for larger colonies: Southern and Southern 1982, Parejo et al. 2006, Zador et al. 2009). The latter problem of variability could be addressed either through sub-colonies or through the use of artificial islands. Most colonial waterbird species are known to nest on dredge spoil (Landin and Soots 1977), and newly created dredge spoil islands offer researchers an opportunity to control more environmental variables than would be possible at naturally formed colony sites. The following discussion provides several examples of how these techniques and others could be adapted to test existing colony persistence theories.



Despite the lack of experimental testing, authors regularly relate their findings on colony turnover rates back to McNicholl's theory (1975) on the importance of habitat stability (e.g., Erwin 1978, Cuthbert 1981, Wesolowski et al. 1985). In the results of the present literature review, this theory seems consistent with observed site use patterns; habitat stability receives unequivocally positive support as a predictor of colony persistence while habitat type receives only moderate support (Table 2). However, habitat stability and habitat type are often intertwined (e.g., Wesolowski et al. 1985). Differences in vegetative cover, substrate type, or human disturbance between habitats can be relatively constant over time, and may be confounded with differences in natural disturbance regimes when studies examine habitat variation as a potential driver of colony persistence patterns. Thus, a scientist wanting to test the predictions of McNicholl's theory (1975) needs to create randomized and controlled treatments that account for or eliminate constant habitat differences. For example, one could compare the responses of birds nesting on adjacent dredge spoil islands to manipulation of substrate stability (e.g., by applying the same overlying material to islands with different foundations such that one degrades faster than the other) or to a change in habitat composition (e.g., by allowing vegetative succession to proceed naturally on some islands while maintaining sparse vegetation on others). As long as experimental colony sites are close together, individuals at the different (sub-)colonies have access to the same food resources and are subject to the same climatic variability. If combined with a rigorous banding program on all islands, a researcher could also test the prediction of group

adherence in unstable habitat by noting whether birds from the unstable colony sites nest with the same neighbors when they change breeding sites.

Similarly, experimental manipulation can be used to determine whether colony size has a causal relationship with colony stability. Both Shields and colleagues (1988) and Brown and Rannala (1995) base their prediction of long-term stability of large colonies on the restrictive assumption that habitat quality does not vary temporally. Invariant habitat quality is a particularly invalid assumption for colonial waterbirds; many species can cause deterioration of their own colony sites over time (Dusi 1979, Ulfvens 1993, Bédard et al. 1995, Peja et al. 1996). However, the social attraction aspect of the theory by Shields and colleagues (1988) can still provide information about colony persistence even when the assumption of invariant habitat quality is relaxed. According to this theory, developed for swallows, individuals choose colony sites by using the number of remnant nests from the previous year as an indicator of breeding success. Because tree-nesting colonial waterbird species build durable nests and may re-use them from year to year (Vergara et al. 2006, Bertolino and Gola 2008), a researcher could artificially augment or decrease the number of old nests in different parts of a colony to determine whether there is a positive relationship between the number of old nests and the number of birds settling in an area. A similar, simpler study has been done by Davis (1986), who determined that Black-crowned Night-Herons (*Nycticorax nycticorax*) and Snowy Egrets (*Egretta thula*) used old nests and trees with old nests before building new nests or using trees from which old nests have been removed. Expansion of Davis' study to include the introduction of "old" nests into trees without old nests would distinguish

between a phenomenon of social attraction (sensu Shields et al. 1988) and high nest-site fidelity.

A controlled study can also provide insights into the robustness of Russell and Rosales' theory (2010), which predicts varying levels of stability for large colony sites depending on individuals' ability to assess colony attractiveness in terms of colony size and carrying capacity. The Purple Heron (*Ardea purpurea*) in Mediterranean France experiences substantial fluctuations in colony size from year to year (Deerenberg and Hafner 1999), which is consistent with the size and occupancy oscillations predicted if individuals are unable to choose the best breeding sites consistently. On the other hand, studies of colonial wading birds in North America find a strong relationship between colony size and stability (Custer et al. 1980, Kirsch et al. 2008) which is consistent with the model if these birds make very accurate assessments of the number of breeding pairs and nesting space and choose colony sites accordingly. If Russell and Rosales' theory (2010) is assumed to be true, then the observed variability in persistence patterns indicates that populations of herons and egrets vary in their ability to assess breeding site quality. One indirect way of testing the model, then, is to determine whether such variation exists in site assessment ability. Researchers with access to two or more dredge spoil islands in the same location can observe the patterns of colony establishment on these islands over several years. As long as the islands are similar in size and composition, evenly-sized colonies across the islands year after year would indicate a high degree of site assessment ability. The islands would have similar carrying capacities and should be settled initially at similar rates, leading late-arriving birds to choose

randomly among sites with similar levels of social attractiveness. If, instead, colony sizes varied greatly between sites within a year and the site of the largest colony varied from year to year, this observation would suggest a lesser degree of site assessment ability. The same procedure conducted in multiple locations would determine whether assessment ability varies between populations. Although this study would not include designated “treatment” groups, the use of dredge spoil islands in the same location would provide the same control over confounding environmental variables that experimental manipulation seeks to achieve.

Without question, the experimental manipulations described above, particularly those involving the creation of artificial habitat, would require a long-term research commitment and ample resources. However, collaboration between researchers, the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service, particularly in the realm of endangered species management, could make this kind of study more realistic. Such collaboration is currently occurring on the Missouri River around the use of artificial and natural habitats by endangered Interior Least Terns (*Sterna antillarum*) and threatened Piping Plovers (*Charadrius melodus*), in this case involving biologists from the U.S. Geological Survey (Sherfy et al. 2008). Knowledge to be gained from such studies is worth the effort and resources. Understanding why colony sites are abandoned is critical information for those involved in wildlife conservation and management, allowing them to predict future site occupancy and plan management actions accordingly. The best way to ensure that these predictions are accurate is to understand the underlying mechanisms determining colony site use.

## THE CASE FOR *IN SITU* STUDY

Robust, all-encompassing theories are often the ultimate goal of science, but in the case of colony persistence, such a theory may be too complicated to compute. The previous two sections have focused on colony persistence patterns as a general phenomenon, but some of the theories described incorporate the role of the local environment or the species of interest in modifying these patterns. McNicholl's theory (1975) provides for regional differences in persistence patterns if regions have different habitat stability regimes, and Russell and Rosales' theory (2010) provides for interspecific differences in persistence patterns if species vary in their ability to choose good colony sites. However, until these theories gain the support of experimental evidence and we understand how spatial and taxonomic variation interacts with general patterns, it would be unwise to automatically generalize influences on colony site dynamics across different situations.

There is strong evidence in the literature for variation in persistence patterns by species and geographic location. Kushlan (1986) provides a vivid example of the former in his study of the differences in colony site use patterns between the Wood Stork and White Ibis (*Eudocimus albus*). The two species breed in the same Everglades habitat; the Wood Stork always uses the same colony sites while the White Ibis frequently changes sites. Kushlan's explanation for this difference comes from the different foraging strategies of the two species; variation in seasonal drying occurs on a spatial scale such that food availability is consistent over time within the Wood Stork's wide foraging range, but is unpredictable within the White Ibis' small foraging radius around colony

sites. When viewed through the lens of McNicholl's habitat stability theory (1975), these species differences show that habitat stability may depend on the way a species uses the habitat rather than being an intrinsic property of the habitat itself.

Ludwig (1962) and Erwin (1978) provide more general examples of species-specific variation in colony persistence patterns. Ludwig (1962) finds qualitative differences in colony site dynamics between four species of colonial waterbirds breeding in the upper North American Great Lakes. Ludwig describes the colony sites of both Herring Gulls (*Larus argentatus*) and Caspian Terns (*Hydroprogne caspia*) as relatively stable, with certain breeding sites used continuously for more than thirty years. Ring-billed Gulls (*L. delawarensis*) show fluctuations in both colony size and location from year to year. Common Terns (*Sterna hirundo*) are described by Ludwig as the species most likely to change colony sites, and of 23 colonies that he surveyed in multiple years, only three had Common Terns for two years in a row. Erwin (1978) observes that colony turnover rates—the proportion of inter-annual colony site changes relative to the overall number of sites used—differ among four species of colonial waterbirds breeding in Massachusetts in 1976 and 1977. The highest colony turnover rates (18%) are found in Least Terns (*S. antillarum*), the lowest (2%) in Herring Gulls, and Common Terns and Black-crowned Night-Herons (*Nycticorax nycticorax*) fall in between (6% and 4%, respectively).

Several examples of location-dependent colony persistence patterns can be drawn from the literature as well, which is not surprising given that different locations may have different habitat types, different waterbird community compositions, different types of

human and natural disturbance, and different distributions of resources. The contrast between two North American Common Tern populations provides a classic case of this phenomenon. The tern colonies of the Northeastern U.S. have been studied extensively throughout the past century (e.g., Austin 1951, Nisbet 1989, Tims et al. 2004) and show such low site turnover (Erwin 1978) that Tims and colleagues (2004) refer to a site at which Common Terns bred for three years as “new” and can compare this site to a colony site that has been used by Common Terns for more than 65 consecutive breeding seasons. As mentioned earlier, Common Terns on the North American Great Lakes are a completely different story. The species is noted as having some of the most variable colony site use of all species in the Great Lakes colonial waterbird community (Ludwig 1962), and less than 7% of sites used by Great Lakes Common Terns during decadal censuses were active in three consecutive census periods (Morris et al. 2010).

A study by Erwin and colleagues (1981) of U.S. Atlantic coast larid colonies provides a combined example of location-specific and species-specific variation in colony persistence patterns. The authors found that New Jersey marsh island colonies of Herring Gulls have almost twice the turnover rate of marsh island colonies of Herring Gulls on the Delmarva Peninsula. In Common Terns, the pattern reverses, with New Jersey marsh island colonies having less than half the turnover rate of colonies on Delmarva marsh islands. Clearly, the characteristics of the species and their environments each have an influence on colony persistence patterns. Application of general theories of colony site dynamics to a specific population and location needs to account for both of

these sources of variation in comparison with the population for which the theory was originally developed.

## CONCLUSION

Given the species-specificity and location-specificity of colony persistence patterns, these patterns may need to be investigated *in situ* if the research is to be directly useful for species conservation and management. In the long run, multivariate modeling studies and experimental testing of causal relationships in colony persistence may be able to tease out the reasons for species-specific and regional differences. Investigators should focus on these two research methods over traditional correlational and univariate modeling studies; although multivariate modeling and experimentation may require more data collection and more resources than univariate studies, they are much better able to determine the factors driving colony persistence patterns. Combined with a cautious approach towards generalization, rigorous research techniques will eventually lead to a more complete understanding of colony site dynamics, which can be used to ensure the continued survival of colonial waterbird breeding colonies.



Table 1. Terms used for subject-based searching of scientific literature databases to identify studies on colony persistence. Synonyms within columns and between columns were connected via Boolean operators OR and AND, respectively.

<u>“Colony” Synonyms</u>	<u>“Persistence” Synonyms</u>
colonial	abandonment
colonies	colonization
“colony-site”	dynamics
colony	extinction
site	occupancy
	persistence
	“site selection”
	“site use”
	stability
	tenacity
	turnover

Table 2. Variables that may influence persistence of waterbird colonies. Positive and/or negative correlation with colony persistence is indicated next to the predictor variable name if directionality is both meaningful and demonstrated in the reviewed research. Studies are classified according to how many predictors of colony persistence were considered simultaneously. “Important” predictors are as defined by the authors of each study; this may or may not correspond to statistical significance.

Predictor variable	Observational studies				Total
	and univariate modeling		Multivariate modeling		
	# studies	# where important	# studies	# where important	
Age of colony (+)	1	1	0	0	1
Colony productivity (+)	2	1	3	0	5
Colony size (+)	16	14	5	3	21
Co-nester presence (+/-)	3	3	2	1	5
Colony isolation (+/-)	1	1	1	1	2
Food resources	0	0	1	0	1
Geographic location	4	4	0	0	4
Habitat area (+)	1	0	2	2	3
Habitat stability (+/-)	12	12	2	2	14
Habitat type	10	6	3	1	13
Human disturbance (-)	2	2	0	0	2
Population trend (+)	1	1	1	1	2
Species identity	11	11	1	1	12
Percent important		86%		57%	

**CHAPTER 2:**  
**SPECIES IDENTITY DETERMINES SITE USE DYNAMICS OF**  
**COLONIAL WATERBIRDS IN THE U.S. GREAT LAKES**

The disappearances and re-appearances of waterbird colonies over successive breeding seasons have fostered dozens of studies attempting to relate site use patterns to both the physical characteristics of colony sites as well as relationships among nesting individuals. Understanding colony site dynamics may be critical to predicting overall population dynamics and to knowing how and where to apply funds and effort for conservation or management. Unfortunately, most previous studies on waterbird colony site dynamics have focused on a single predictor at a time and its relationship with site colonization or re-use probabilities. Because an individual or group's experience at a nest site may be a product of complex interactions among many facets of the environment, both physical and biological, these earlier studies may not provide the most meaningful representations of their study systems.

The colonial waterbird community of the North American Great Lakes is an excellent system in which to explore the interaction of multiple environmental factors on site use dynamics of colonial waterbirds. The community is diverse, including sixteen species from three orders (Pelecaniformes, Suliformes, and Charadriiformes). Four decadal censuses of Great Lakes colonial waterbirds provide a record of colony site use spanning 30 years as well as ancillary data on colony site characteristics and changes over time. Finally, a better understanding of colony site dynamics in this community is

needed to help address the real conservation and management issues that exist for many species, including the decline of marsh-nesting terns (Cuthbert and Wires 2011) and management of the Double-crested Cormorant population (*Phalacrocorax auritus*; Weseloh et al. 2002).

The objective of my study was to identify predictors of site colonization and colony persistence probabilities for U.S. Great Lakes colonial waterbirds. I addressed this question using a hierarchical model of community occupancy dynamics (Royle and Dorazio 2008) to examine the relative impacts of a variety of predictors while also accounting for the possibility of failure to detect all species present at active colony sites.

## Hypotheses

I predicted that site colonization and the persistence of active colonies from one census to the next would be influenced by both the physical and social environment at the colony site. The model included six covariates associated with the physical environment: landform of the colony site, distance of island sites from the mainland, distance of the site from human access points, nesting substrate vegetation, flooding potential, and the proportion of area within a 5 km radius of the site that was developed land. The model also included four variables dealing with the birds' social environment: historical nest abundance, historical site species richness, regional population trend, and species identity. Through analysis of previous literature, I developed expectations about the direction of impact of each factor on colonization and/or persistence of colony sites.

*Landform and distance to the mainland.*—The landform of a colony site, i.e., whether it was on an island or on the mainland, could approximate the influence of terrestrial predators on a colony site, while the distance of a site from the mainland could indicate availability of shallow water food resources. Mainland sites should have been highly accessible to mammalian nest predators, with the exception of some coastal marshes. Burger (1982) reported that Black Skimmer (*Rynchops niger*) colonies with little to no reproductive success were particularly unlikely to reoccupy the same sites in the future if reproduction was limited by predation as opposed to flooding. Accessibility of island sites to terrestrial predators should decline with distance from the mainland, but near-shore sites are also closer to the shallow water habitats in which many species, both divers and waders, feed (Dorr et al. 2010, Lantz et al. 2010). Thus, I predicted that island sites would be used more frequently than mainland sites for colonial waterbird breeding, while islands close to the mainland would be used more than sites further away.

*Developed land and accessibility.*—Human disturbance at a colony site was measured by the amount of developed land around the site and the ease with which people could access the site. I included the former variable as a predictor of colonization probability and the latter as a predictor of persistence probability; low resource availability ensuing from development may be part of the colonizers' decision to settle or not at a particular breeding site, while human visitation may be more obvious to established breeders than to prospectors. Disturbance can have a strong negative effect on colony persistence (Creutz 1967, Burger 1984, Fasola and Alieri 1992) but susceptibility

to human disturbance also varies by species (Nisbet 2000). Thus, I expected to find a generally negative relationship between site use and each disturbance metric along with species-level variation in the strength of the relationship.

*Substrate vegetation.*—Due to the long interval between occupancy surveys for Great Lakes waterbird colonies, which occur approximately once per decade, vegetative succession could cause sites to become unsuitable for certain species from one census to the next. I expected the nesting substrate for a colony of a given species to affect its persistence in a species-specific way. For example, Caspian Terns (*Hydroprogne caspia*) nest on bare substrates (Ludwig 1965). This species may abandon vegetated substrates more frequently than sites without vegetation, because vegetated sites are more likely to transition to a habitat with woody vegetation within the decade between surveys.

*Flood potential.*—Loss of a colony site to flooding is an extreme example of habitat change that precludes future nesting. A number of Great Lakes waterbird colonies occur on shoals (Cuthbert and Wires 2011), and I predicted that the ability of these sites to disappear in the interval between censuses would necessarily decrease persistence probability of the colonies that nested on them.

*Colony size.*—Larger colonies persist longer (e.g., Buckley and Buckley 1982, Parejo et al. 2006, Kelly et al. 2007) with few exceptions in the literature (Erwin et al. 1998, Martinez-Abrain et al. 2003, Scarton 2008). Thus, I expected to find a positive

relationship between colony size and colony persistence in Great Lakes colonial waterbirds.

*Species richness.*—Field research on interactions between species of waterbirds has generally been limited to study of the negative influence of one species on another. However, observations of diverse colonial waterbird communities on the Atlantic coast of the United States suggest that colonies with more species are more persistent (Custer et al. 1980, Bancroft et al. 1988), which could be due to the diversity of resources available at the colony site or because individuals of different species compete less directly for resources but can still reap predator defense benefits from nesting together (Burger 1981). Given the diverse community of colonial waterbirds in the Great Lakes, I expected to see colony sites with a history of high species richness colonized and reoccupied more often than those sites without high species richness.

*Regional population trend.*—Intuitively, species with growing populations should colonize more sites and species with declining populations should abandon more sites than populations that are stable. Erwin (1978) reported this pattern in colonial waterbirds nesting in Massachusetts, and I predicted a similar pattern in Great Lakes colonial waterbirds, which have experienced population declines and increases over the period of occupancy records.

*Species identity.*—Species identity is incorporated into many of the variables described above. Even in the same habitat, patterns of colony site use can vary considerably among species due to differences in life history strategies (Kushlan 1986). With the diversity of species and life histories present in the Great Lakes colonial waterbird community, I expected to find frequent differences in the strength of relationships between predictor and response.

## METHODS

### Site occupancy records

Occupancy histories of potential waterbird colony sites in the U.S. Great Lakes were obtained from the U.S. database of the Great Lakes Colonial Waterbird Survey (GLCWS). The U.S. Fish & Wildlife Service, the Canadian Wildlife Service, professional and amateur ornithologists, and government agency cooperators collaborated to conduct the GLCWS approximately once per decade from 1976 through 2010, with survey periods as follows: 1976-1977 (Scharf 1978), 1989-1991 (Scharf 1998, Scharf and Shugart 1998), 1997-1999 (Cuthbert et al. 2010), 2007-2010 (Cuthbert and Wires 2011). Details on GLCWS methods can be found in the report of the fourth survey (Cuthbert and Wires 2011). The present study included sites located between Pigeon Point, Minnesota, and Three Mile Bay, New York, in the U.S. waters of the five Great Lakes (Superior, Michigan, Huron, Erie, and Ontario) and their connecting waterways (St. Marys River, Detroit River, Lake St. Clair, and Niagara River). The study area boundary of the GLCWS is set as 1 km inland from the shoreline of each of the above water bodies. I



excluded 28 known colony sites within the study area for which I could not determine a reasonably accurate location. The final dataset included 659 sites, each with occupancy histories for the ten colonial waterbird species of interest during each of the four surveys. In addition, the occupancy status of approximately 4% of site-year combinations were recorded multiple times (2-4) within a single year. I defined a site as occupied by a given species if it contained the nest of one or more breeding pairs of that species; similarly, a colony was defined as one or more nests of a single species breeding at the same site. This definition reflects the assumption that if at least one pair nests at a given site, then that site is somehow attractive to members of the species in general. The same definition has been used by several other colonial waterbird researchers (e.g., Buckley and Buckley 1982, Barbraud et al. 2003, Chaulk et al. 2006) although a variety of other definitions are also commonly applied (e.g., Custer et al. 1980, Burger 1982, Bryan et al. 2003, Scarton 2008).

### Study species

Sixteen species of colonial waterbirds have been documented breeding in the U.S. Great Lakes since the first GLCWS survey period in 1976-1977 (Cuthbert and Wires 2011). I chose to focus my modeling efforts on the ten species for which there were at least 30 records of confirmed breeding across the four surveys. These ten species were: Black-crowned Night-Heron (*Nycticorax nycticorax*; "BCNH"), Black Tern (*Chlidonias niger*; "BLTE"), Caspian Tern ("CATE"), Common Tern (*Sterna hirundo*; "COTE"), Double-crested Cormorant ("DCCO"), Forster's Tern (*S. forsteri*; "FOTE"), Great Blue

Heron (*Ardea herodias*; “GBHE”), Great Egret (*A. alba*; “GREG”), Herring Gull (*Larus argentatus*; “HERG”), and Ring-billed Gull (*L. delawarensis*; “RBGU”).

#### Covariate values

The GLCWS census yields the number of apparently occupied nests for each species at each breeding site, which supplied me with estimates of nest abundance as well as study-wide population trend, obtained by comparing total nest abundance between censuses. “Nest abundance” as used in the present study describes the number of nests of a single species, which is not the same as the total number of nests at mixed-species colony sites. The site occupancy records provided estimates of historical species richness, which I defined as the number of other species (relative to the species being modeled) recorded at a given site in the previous census period. Additional data recorded by GLCWS observers provided me with most covariate values for vegetation and flooding potential. Nesting habitat was coded as bare of vegetation if the observer had given no indication of vegetation and described the substrate as “unvegetated,” “unbroken rock,” “bare,” “boulders,” “sand/gravel,” “rock rubble,” or a solid artificial substrate like concrete. A site had potential to be flooded if nesting elevation was always within 2 m of water level, if the observer noted flooding as a potential threat to nesting, or if the observer noted that the site was actually flooded in one or more surveys. Missing data on vegetation and flood potential were supplied by expert opinion or examination of the GLCWS’ aerial photography of colony sites. Google™ Earth satellite imagery was used to supply data that were otherwise unavailable.

I used ArcGIS Desktop (Esri) tools to obtain covariate values for site distance to the mainland, isolation from human access, and the proportion of developed land within a 5 km radius. The GLCWS database provided coordinate locations of each site; given that many of these locations were recorded from moving aircraft in the 1970s and 1980s, I assumed their accuracy to be no better than 0.1 km. I used the National Oceanic and Atmospheric Administration's (NOAA) Raster Navigational Charts to define the location of the Great Lakes shoreline and then measured the distance of each island site from this boundary within the UTM coordinate system centered nearest the site (see Appendix 2 for electronic data sources used in spatial analyses). The definition of the shoreline according to the NOAA navigational charts often placed coastal marshes on the mainland side of the shoreline. Similarly, I obtained data on public boat access points to the Great Lakes from the relevant state government departments of natural resources (Appendix 2) and measured distance between each colony site and the nearest access point. Mainland sites along the shore that had no human development within 0.1 km were treated the same way as island sites. Mainland sites in close proximity to development were assigned an access distance of 0. To determine extent of developed land near colony sites, I obtained land use/land cover data based on 1970-1985 aerial imagery from the US Geological Survey (USGS; Appendix 2) and 1996 and 2006 land use/land cover data from NOAA's Coastal Change Analysis Program (Appendix 2). I selected polygons representing all developed land out of these datasets and calculated the proportion of the area within a 5 km radius of each colony site that was covered by these polygons. The 5 km radius was chosen because it is the landscape scale at which roads, a form of low-intensity

development, influenced colony site selection of Double-crested Cormorants in the Great Lakes in a study by Trexel (2002).

#### Statistical analyses

*Model specification.*—The present model of colony site occupancy dynamics was based on a model of community dynamics developed by Royle and Dorazio (2008), selected for its ability to deal with incomplete detection of active colonies and a community of species about which varying amounts of information are available. This model exploits repeated visits to the same site within a season to distinguish the probability of detecting an active colony from the probability that the colony is active. Thus, the model is hierarchical, consisting of a sub-model describing the process of detecting occupancy states (“detection sub-model”) layered over a sub-model describing the partially observable true occupancy states of colony sites (“occupancy sub-model”).

In the detection sub-model,  $y_{species,site,census}$  denotes observed detection history, indexed by species, site, and census period. The variable  $y$  has a binomial distribution, where the number of “trials” is the number of same-year visits to the colony site, denoted as  $J_{species,site,census}$ . The binomial success probability is a function of  $p_{species,site,census}$ , the species-, site-, and census-specific probability of detection, and  $z_{species,site,census}$ , the true occupancy status of the site for the given species and census, such that the binomial success probability equals 0 if  $z = 0$ :

$$y_{species,site,census} \sim \text{Binomial}(x_{species,site,census}, J_{species,site,census})$$

$$x_{species,site,census} = p_{species,site,census} \times z_{species,site,census}$$

In the occupancy sub-model,  $z_{species,site,census}$  denotes the true species-specific occupancy state of a site in a given year. For the first census period,  $z_{species,site,1}$  is defined as a Bernoulli random variable with success probability  $\psi_{species}$ , or, the species-specific initial occupancy probability:

$$z_{species,site,1} \sim \text{Bernoulli}(\psi_{species,site})$$

In subsequent census periods,  $z_{species,site,census}$  is defined as a Bernoulli random variable with a success probability equal to the persistence probability of the colony ( $\phi_{species,site,census}$ ) if the site was occupied in the previous census, and equal to the colonization probability of the site ( $\gamma_{species,site,census}$ ) if the site was unoccupied in the previous census:

$$z_{species,site,census} \sim \text{Bernoulli}(\pi_{species,site,census})$$

$$\begin{aligned} \pi_{species,site,census} = & z_{species,site,census-1} \times \phi_{species,site,census} \\ & + (1 - z_{species,site,census-1}) \times \gamma_{species,site,census} \end{aligned}$$

Thus, occupancy becomes a first-order Markov process, where the species-specific occupancy state of a given site depends on its species-specific occupancy state in the preceding census.

Hypotheses about site-specific covariates affecting colonization and persistence probabilities were incorporated into the detection and occupancy sub-models using the logit link (see Appendix 3 for full model specification). In addition to covariates discussed previously, the function describing colony persistence probability also included a location-specific random effect, which improved convergence of Markov chain Monte Carlo simulations (see Model Analysis). Because I hypothesized that detection rates were

higher for larger colonies, I defined  $p_{species,site,census}$  as a logit-linear function of a species-specific constant term and species-specific nest abundance ( $abs_{species,site,census}$ ):

$$\log\left(\frac{p_{species,site,census}}{1 - p_{species,site,census}}\right) = a0_{species} + a1 \times abs_{species,site,census}$$

Concern about the validity of assuming that site occupancy remains constant throughout a season (Rota et al. 2009) led me to test for an effect of visit interval length on detection rate using simple logistic regression. Because this test yielded a non-significant result (see Results), visit interval was not included as a covariate in the final model.

Species-specific responses to covariates were modeled like normally-distributed random effects around the community's "average" response. For example:

$$a0_{species} \sim Normal(mu. a0, sigma. a0)$$

This assumption allowed the responses of species for which many data were available to inform estimates for species with fewer data. Structuring species-specific responses in this way is reasonable because the biology of all waterbird species is similar to some degree, with variation among species according to variation in life history strategies.

*Model analysis.*—I analyzed the colony site dynamics model within a Bayesian framework using Markov chain Monte Carlo (MCMC) simulation. I assigned flat prior distributions to each stochastic node in the model. For the hyper-parameters describing the normal distributions of species' responses to covariates, these priors were normal (mean = 0, variance = 2.5; an approximately flat prior on the logit scale) for the mean of the distribution and uniform in the range of 0 to 10 for its variance. Initial values for the simulation were generated randomly from the prior distribution assigned to each

parameter, and these values were adjusted if necessary to obtain a broad distribution of starting values across the different chains.

MCMC simulations were carried out using the program WinBUGS (Lunn et al. 2000) with a Metropolis-Hastings algorithm. I ran four simultaneous chains until the MCMC error for all monitored parameters was less than 5% of the estimated standard deviation of the posterior distribution. I discarded the first 20,000 iterations of each chain as burn-in and thinned the chains by 50 iterations after monitoring autocorrelation functions. I assessed convergence of the chains both visually and by monitoring the Gelman-Rubin R-hat statistic (Gelman and Rubin 1992). The final length of the chains was 250,000 iterations, with 18,400 values used for model inference. The “CODA” package (Plummer et al. 2006) in program R (R Development Core Team 2010) facilitated posterior inference. In the results text, posterior parameter densities for parameters that are naturally interpreted as probabilities are reported on the probability scale. Other posterior parameter densities associated with logit-linked covariates are described on the odds scale.

Model fit was evaluated using Bayesian p-values (King et al. 2010). I generated simulated data on colony detection for each site and census period from the observed covariate values and the parameter estimates of 1000 randomly selected MCMC iterations from each of the four chains. The negative log-likelihood was used as the discriminant function. By this method, model fit is good when the evaluated discriminant function for the simulated data is larger than the evaluated discriminant function for the observed data in approximately 50% of iterations, or a p-value of 0.5 (King et al. 2010).

## RESULTS

Colony detection probability in the GLCWS was a function of both species identity and nest abundance. The estimated mean of the distribution of detection probabilities across all species was 0.635 (95% credible interval: 0.429-0.807) for a colony of 48 nests (mean colony size across all species). For every standard deviation (923 nests) increase in nest abundance, odds of detection were multiplied by 2.1 (95% credible interval: 1.758-2.566). The lowest mean estimate of detection probability for a colony of 48 nests was 0.18 for Ring-billed Gulls (95% credible interval: 0.14-0.234). However, the average-sized Ring-billed Gull colony (4027 nests) was detected with a mean probability over 0.8, and colonies of 10,000 nests and above, of which there were 27, had detection probabilities of approximately 1 (Fig. 1A). Mean detection probability estimates for all other species were  $> 0.5$  for the mean colony size. Black Terns had the highest detection probability for a colony of 48 nests, with a mean parameter estimate of 0.89 (95% credible interval: 0.684-0.986) and little change in detection probability over the range of observed colony sizes (Fig. 1B). The probability of consistent detection of an active colony was not a function of the length of time between successive within-season site visits (likelihood ratio test,  $\chi^2 = 1.29$ ,  $df = 1$ ,  $P = 0.256$ ), suggesting no major violation of the assumption of within-season “closure” of sites to changes in occupancy.

Initial occupancy probabilities represented the probability of site occupancy in the first survey period for sites that were reported as occupied by colonial waterbirds at some point across the four censuses. Distributions for initial occupancy probabilities showed Herring Gulls and Ring-billed Gulls as potentially occupying between one quarter and



one half of potential colony sites, while Common Terns were estimated to occupy between 10 and 20% of potential colony sites, and the remaining species were estimated to occupy less than 10% (Fig. 2). Apparent occupancy rates in the first census period were either below or within the confidence interval for estimated initial occupancy probability for all species. The difference between apparent occupancy and estimated true occupancy was greatest for Herring Gulls and Ring-billed Gulls, with apparent occupancy rates of 0.29 and 0.07, respectively.

Fit of the colony site dynamics model to GLCWS data on colony detection was good, with a Bayesian p-value of 0.47. The p-value suggests that the model was able to capture much of the variation in colony site use dynamics for this waterbird community. However, breaking down the model into parts corresponding to each species demonstrated that the model provided much better fit for some species than for others (Table 1).

#### Influences on colonization probability

The intercept of the logit-linear model for colonization probability represented the log-odds of colonization of mainland sites with no surrounding development and no other nesting species when the regional population was not increasing; the probability of colonizing a site under the above conditions is referred to in the following discussion as “baseline” colonization probability. The model demonstrated considerable variation in species’ baseline colonization probabilities for potential colony sites. Herring Gulls had the highest baseline colonization probabilities (95% credible interval: 0.098-0.204) and

Caspian Terns had the lowest (95% credible interval: 0.0-0.004). Common Terns and Ring-billed Gulls also had relatively high baseline colonization probabilities (both with an estimated mean probability of 0.021). As expected, an increasing regional population multiplied the odds of colonization of individual sites by 2.545 (95% credible interval: 1.863-3.575).

Species-level variation was apparent in colonization responses to each of the environmental predictors considered. Black Terns were the only species that exhibited consistently higher odds of using mainland sites (including some coastal marsh sites) compared to island sites; Great Egrets showed a similar but weaker pattern (Table 2). The odds ratio for colonization of island sites over mainland sites was high for Double-crested Cormorants, Forster's Terns, and Herring Gulls; the remaining five species showed a weaker tendency to use island sites. Although on average, the odds of colonization by the waterbird community were higher for island sites (mean: 1.575, 95% credible interval: 0.654-3.877), most of the probability density for the average community response to distance from the mainland suggested higher odds of using near-shore sites (mean: 0.653, 95% credible interval: 0.363-1.104). Indeed, Herring Gulls were the only species for which the odds of use increased with distance from the Great Lakes shoreline, and the odds of use clearly declined with distance from the mainland for Black Terns, Common Terns, and Forster's Terns (Table 2).

For the two gull species, the odds of site colonization increased when a greater proportion of the surrounding land was developed, while the model suggested greater odds of use of undeveloped land by the two marsh terns (Black Tern and Forster's Tern;

Table 3). The remaining species fell in between these extremes, with probability density concentrated on the side of greater development for Black-crowned Night-Herons, Great Egrets, and Common Terns, and on the side of less development for Caspian Terns, Double-crested Cormorants, and Great Blue Herons.

#### Effect of species richness on colonization and persistence

The effect of species richness on the odds of colonization varied by species; the variance of the posterior distribution of species responses to historical site species richness (mean: 2.121, 95% credible interval: 1.121-4.159) was higher than the variance of any other posterior distribution of species responses to factors affecting colonization probability. Combined analysis of the effect of species richness on both colonization probability and persistence probability suggests that there are two distinct types of responses to the presence of other nesting species at the colony site (Fig. 3). One group, including Herring Gulls and three of the four tern species, tends to colonize sites without other species and may or may not persist at sites where other species are present. The other group, including Caspian Terns, Double-crested Cormorants, and all of the ardeids, tends to both colonize and persist at sites where other species also nest. Although the mean response of Ring-billed Gulls is more similar to the second group, the posterior distribution for the colonization odds has an extremely wide spread (95% credible interval: 0.005-7.301).

#### Influences on persistence probability

Historical nest abundance at a colony site had by far the greatest influence on the return of a species to that site in the next census period; in the mean community response, odds of persistence were multiplied by 24.754 (95% credible interval: 1.303-463.126) for each standard deviation (923 nests) increase in the number of nests. Variability in response was high both among species (95% credible interval for community variance parameter: 8.067-9.986) and among colonies of a given species (Table 4). Both species with small median colony sizes (Black Tern, Great Blue Heron, and Herring Gull) and species with large median colony sizes (Double-crested Cormorant and Ring-billed Gull) showed unequivocally positive responses to increasing colony size in terms of their odds of persistence.

Colonies on sites with potential to become inundated with water had lower odds of persistence than colonies on sites that were not vulnerable to flooding (mean: 0.694, 95% credible interval: 0.481-1.001). Unlike the positive relationship between increasing population trend and colonization probability, a declining regional population trend did not clearly reduce the odds of persistence (mean: 0.907, 95% credible interval: 0.622-1.326).

Neither substrate vegetation nor site isolation from human access had strong effects on colony persistence (Table 5). The variance among species in response to these variables was quite low (vegetation, 95% credible interval: 0.023-1.965; access, 95% credible interval: 0.009-0.679). Mean estimates of the response to isolation from access indicated a positive relationship between distance from access points and persistence

probability in all species, but all parameter distributions had considerable density to suggest a negative or neutral relationship was possible as well.

## DISCUSSION

Although colonial waterbirds of different species may use the same colony sites and be influenced by the same site environment, it is clear from the results of my model that each species responds to this environment in a unique way. For nearly every environmental covariate included in the model for which response was allowed to vary by species, I observed such variation. The direction of response to many of the predictors agreed with my hypotheses and the previous literature, but in some cases species responded in unexpected ways.

Historical nest abundance was the strongest predictor of colony persistence across the Great Lakes colonial waterbird community. This result was expected and agrees with the patterns seen in many other species and geographic regions (e.g., Buckley and Buckley 1982, Parejo et al. 2006, Kelly et al. 2007). The mechanism for this relationship is unknown, but if assuming at least moderate individual site fidelity, explanations could include attraction among conspecifics, higher reproductive success in larger colonies (but see Parejo et al. 2006, Lombard et al. 2010), and that demographic stochasticity is more likely to result in extinction of small colonies as compared to large ones (Robertson et al. 2007). However, abundance could also be a correlate of some other environmental variable, e.g., availability of a particular resource that drives persistence at colony sites instead of abundance itself being directly related to persistence. Such a set of

relationships could explain the observed high degree of variability in response, because if abundance and this hypothetical variable were not perfectly correlated then there would be more observed variation in response to abundance than in response to the hypothetical variable actually driving persistence.

I did not expect the pattern of community responses to developed land area around the colony site to be different from the pattern of responses to site isolation from human access. Both variables were intended to measure human disturbance at a colony site, with developed land area determining colonization probability and isolation important in persistence probability. Although some species appeared to be more sensitive to developed land than others, all species responded slightly in favor of greater access distances (Tables 3, 5). A possible explanation for this pattern is that species sensitivity to human disturbance is most important in colonization of new sites; if birds nest only at sites with tolerable amounts of disturbance then there will be less variation in levels of disturbance among active colony sites than among all possible colony sites.

I expected to find much more variability in response to substrate vegetation than was actually observed. For instance, Caspian Terns and Common Terns nested on bare substrates at 71% and 58% of their colonies, respectively, and because Caspian Terns were never found nesting in woody vegetation and Common Terns only twice, I expected they would be more persistent at sites with bare substrates. Sites with vegetated substrates should reach a successional stage with woody vegetation faster than sites with bare substrates, and therefore become inappropriate sites for tern colonies within a shorter period of time. That I did not observe such patterns is likely due to the simplicity of the

vegetation metric. GLCWS observers recorded colony site habitat in such terms as “upland,” “wetland,” or “artificial,” and then noted the particular nesting substrate. Therefore, it is unknown from GLCWS data whether a single site is relatively uniform habitat or whether it has multiple areas with different vegetative communities. If colonies can move within a site in response to changes in vegetation, they may be able to persist even when the original nesting location is no longer ideal. Because details of vegetation such as size were often noted in GLCWS surveys, it is also possible that setting a different cut-point other than “non-vegetated” versus “vegetated” would lead to more informative results on the response of colonies to site vegetation. Including more detail on vegetation was not feasible for this analysis given the already-substantial size of the model. Thus, although multivariate analyses are critical to understanding the big picture of colony site persistence, understanding the influence of site vegetation may be an area in which detailed study of that single aspect of a colony’s environment could yield more valuable information.

The finding that there were two relatively distinct responses to colony site species richness is novel and interesting. According to these results (Fig. 3), only certain species frequently colonize and persist at sites where additional species also breed. Considering the life histories of different species may provide insights into this pattern. Three of the four tern species occurred in the group of species that tend to nest alone. The wetland breeding habitat of Black Terns and Forster’s Terns is an uncommon breeding habitat for other species in the Great Lakes colonial waterbird community, so the finding that marsh terns nest alone is not particularly surprising. Common Terns breed in the same types of

habitats as several other species, so their frequent use of single-species colony sites could instead arise from their interactions with other species, several of which will out-compete them for nest sites or depredate their nests (Morris et al. 1992, O'Connell and Beck 2003, Hall and Kress 2008). Double-crested Cormorants, the three ardeids, and Caspian Terns all appeared in the group that uses colony sites with a history of colonial nesting by other species. Burger (1981) hypothesizes that mixed-species breeding colonies allow individuals to benefit from the predator protection achieved by colonial nesting while reducing resource use overlap among members of the colony. Although nest site competition may occur among these species (Burger 1979), they do not regularly depredate each other's nests, such that the advantages of mixed-species colonies may outweigh the disadvantages. The two gull species are both interesting cases: Ring-billed Gulls appeared most similar to the group that breeds in mixed-species colonies but they exhibited huge variability, and Herring Gulls colonized empty sites but persisted at sites where other species were also nesting. These ambiguous results may be due in part to the ability of gulls to nest both in urban areas, where no other species commonly nests, and on more remote islands. With such flexibility in behavior, separate analyses of urban colonies and remote colonies might provide a better understanding of whether the reaction of gulls to heterospecifics is dependent on other features of their environment.

The Bayesian p-value measure of goodness of fit for the present model suggests that it incorporated most characteristics of colony site environments that are relevant to the prediction of community site use dynamics. However, fit was not as good for the models of many of the individual species (Table 1), suggesting that some possibly



influential characteristics were missed. These could include management, either of site vegetation or of nest success, and presence of introduced predators at island colony sites. A complete dataset is not available for either of these site characteristics in the Great Lakes, but management has been applied in many forms by many different entities (Morris et al. 1992, Bédard et al. 1995, Cuthbert and Wires 2011), and colony site abandonment has been observed following the introduction of terrestrial predators (F. Cuthbert, pers. comm.). Additionally, the form of the detection sub-model likely contributed to particularly poor model fit for Herring Gulls, where the p-value suggested over-fitting, and Ring-billed Gulls, where the p-value suggested under-fitting. I did not allow interspecific variation in the model term for the effect of abundance on detection probability because of sparse data and poor convergence of models allowing such variation. However, Herring and Ring-billed Gulls represent the opposite ends of the spectrum in terms of colony size and may demonstrate the inability of one parameter to capture the entire range of species responses. Herring Gulls are often found nesting alone and nearly one-third of colonies detected by the GLCWS had fewer than 10 nesting pairs. Based on the means of the posterior parameter distributions, the detection probability for a single Herring Gull nest is over 60%, a probability that seems unreasonably high given the vastness of the study area and the observation that Herring Gulls nested in vegetation at over 40% of detected colonies. In contrast, the average size of Ring-billed Gull colonies was several times larger than the average colony size of any other species, leading to unreasonably low estimated detection probabilities for colonies of even 1000 nests (Fig. 1A). Better-fitting models for these species are likely possible given the

relatively large amount of data available on each, but would require a more directed approach towards the species of interest than was taken in this study.

#### Evaluation of assumptions

The model used to predict colony site dynamics in the present study makes a key assumption about the “closure” of a site to occupancy changes within a season. If true occupancy can change within a season, then it is impossible to know whether failure to detect a colony observed to be active on another visit is truly due to detection failure or whether detection is accurate but the colony is no longer active at that site. Rota and colleagues (2009) demonstrate that when the assumption of closure is violated, occupancy rates will be overestimated. They recommend shortening the time between within-season site visits to minimize the probability of closure assumption violation. Although birds may move between colony sites over the course of a single breeding season (Cuthbert 1985), I found no relationship between the interval between within-season visits and the rate of colony detection in the GLCWS data, which suggests that violation of the closure assumption was not a major problem for my model.

A second major assumption of the model was that colony site use depends on conditions at a prior time period, a situation known as Markovian dynamics. More specifically, the first-order Markov process assumed in the model states that site use in census  $k$  depends on site use in census  $k - 1$  alone. Evidence that birds visit and select colony sites in the season prior to breeding (Dittmann et al. 2005) and some modeling work (Barbraud et al. 2003) suggest that colony site dynamics are often Markovian, but

not all tests for Markovian dynamics find the same result (Erwin et al. 1998). Further support for the frequency of Markovian dynamics in colony site use comes from myriad studies that exhibit connections between some characteristic of a colony and its occupancy in the following year. These studies do not provide robust tests for Markovian dynamics because environmental variables may be correlated across years with birds responding to within-year conditions, but at a minimum they do not provide evidence against Markovian dynamics. A prior test of Markovian dynamics in Ring-billed Gull site occupancy over the decadal timeframe of the GLCWS strongly supported a Markovian model over a non-Markovian alternative (K. E. Wyman unpubl. data). It seems most plausible that Markovian dynamics of colony sites in the Great Lakes truly depend on shorter intervals of time, on the order of one or two years rather than a decade because only a small number of individuals would remain in the breeding population from one decadal survey to the next. However, the connection between time periods appears to be strong enough to link environments between census periods and generate relationships between site conditions in the previous census period and occupancy in the current period. At the same time, the small number of individuals breeding in multiple censuses reduces the influence of individual site fidelity on colony persistence, so that colony persistence between censuses is more a reflection of site environment than individual experience.

Due to limitations of the available data, I could not estimate separate detection probabilities over each survey period and had to assume that detection probability was constant over time, except in response to variation in nest abundance. Because of the long

history of study of colonial waterbirds in the Great Lakes and reliance on wildlife and avian professionals to perform surveys and censuses for the GLCWS (Cuthbert and Wires 2011), this assumption seems reasonable. Similarly, in an analysis of 317 North American Breeding Bird Survey route-years, species-level variation was the dominant source of detection probability heterogeneity, and was the only source of heterogeneity on nearly two-thirds of route-years to the exclusion of heterogeneity due to time, location, and observer experience (Boulinier et al. 1998).

#### Implications for conservation and management

With thirteen of the sixteen U.S. Great Lakes colonial waterbird species listed as endangered, threatened, or of special concern in at least one Great Lakes state (Cuthbert and Wires 2011) and the remaining three species prioritized for management or stewardship in the region (Wires et al. 2010), conservation and management are important issues for Great Lakes colonial waterbirds. Some of the most relevant conservation-related findings of this study are those on the relationship between colony size and persistence, the location-dependence of site use probability, and species-level variation. The model demonstrated that colony size is not only a predictor of colony persistence, as many studies have reported, but that it is a considerably stronger predictor of persistence than many other potential predictors. Therefore, colony size is a good starting point in prioritizing colony sites for targeted conservation or management, such as obtaining conservation easements on sites. Depending on the species of interest, species richness of colony sites can also factor into site prioritization. The results on site

colonization probabilities relative to landform and distance from the mainland demonstrate that only one species, the Herring Gull, colonizes isolated islands more frequently than near-shore sites, implying that all other species nest in locations that are likely to bring them into conflict with human land uses. Finally, across nearly all predictors of both colonization and persistence, species showed unique responses to their social and physical environment. Thus, conservation and management need to be tailored to particular target species; general conservation and management schemes will likely be less effective.

The above suggestions for applying the present study's findings can be illustrated with brief case studies of Common Tern conservation and Double-crested Cormorant management in the Great Lakes. Common Terns in the Great Lakes exhibit particularly high colony turnover compared to other species in the Great Lakes and compared to Common Terns breeding elsewhere (Ludwig 1962). Common Terns are either endangered or threatened in all but one Great Lakes state (Cuthbert and Wires 2011) and have also experienced declines in Canada as tracked by the Canadian portion of the GLCWS (Morris et al. 2010). My results for Common Terns suggest that conservation should focus on three major issues for this species: protecting and managing sites with large colonies due to their high probability of persistence, protecting active colony sites with low flooding susceptibility as terns often nest on transient sandy shoals, and managing co-nesting species to reduce negative interspecific interactions at shared colony sites. Many of these methods are already used in Common Tern conservation in the Great Lakes region (Morris et al. 1992), so the present study serves to reinforce those practices.

Management of Double-crested Cormorants in the U.S. Great Lakes is generally conducted with the goal of reducing impacts on fisheries and site vegetation and consists of oiling eggs or shooting adults at the colony site (Bédard et al. 1995, Dorr et al. 2010). In the model results, cormorants showed a positive response to the presence of other species, both in site colonization and colony persistence probabilities. Thus, managers must bear in mind that cormorant control activities are very likely to disturb other species nesting at the same colony site, the consequences of which have not yet been adequately addressed through scientific study (Wires and Cuthbert 2006). If cormorant population reduction is desirable, then management should focus on large colony sites to reduce the number of colonies at which management disturbance must occur and to improve efficiency by managing the same sites for multiple years in succession.

It has been acknowledged both theoretically (Diamond and May 1977) and in practice (Erwin 1978, Frederick and Meyer 2008) that the apparent turnover rate of species or colonies in habitat patches declines as census interval lengthens. In the present study, occupancy was only measured about once every ten years even though sites were occupied annually. Due to the complexity of modeling all possible yearly occupancy histories between the decadal surveys, I chose to model the probabilities of colonization and extinction on a decadal rather than a yearly basis. This choice has arguably more relevance for conservation, as conservation practitioners will want to ensure that their choices support species survival in the long rather than the short term. However, decadally-based predictions of colonization or persistence will not translate easily to questions of inter-annual colony persistence. Thus, the site occupancy state of any given

Great Lakes colony probably changes much more frequently than is detected by the GLCWS, and colonies may disappear from sites much more often than expected. This situation is challenging for conservation, because funding sources typically expect short-term results that are not always realized despite well-informed management practices (Morris et al. 1992). In reality, the abandonment of a colony site for a year does not mean that the birds will not return frequently to that site in the future, and using the variables most strongly correlated with decadal colonization and persistence probabilities for each species can improve the odds that recolonization will occur.

Table 1. Bayesian p-values for the present model of site use dynamics of Great Lakes colonial waterbirds, partitioned by species.

Species	p-value
Black-crowned Night-Heron	0.387
Black Tern	0.459
Caspian Tern	0.555
Common Tern	0.340
Double-crested Cormorant	0.734
Forster's Tern	0.261
Great Blue Heron	0.459
Great Egret	0.640
Herring Gull	0.015
Ring-billed Gull	0.964



Table 2. Posterior means and 95% credible intervals for parameters measuring the effects of landform (island or mainland) and distance to the mainland on site colonization probability for Great Lakes colonial waterbirds. A one-unit increase in distance from the mainland in the model is equivalent to a 12 km increase in distance on the ground. See “Methods” for species name abbreviations.

Species	Island landform		Distance to the mainland	
	Posterior mean	95% credible interval	Posterior mean	95% credible interval
BCNH	0.38	(-0.70, 1.57)	-0.43	(-1.06, 0.12)
BLTE	-1.37	(-2.05, -0.72)	-1.07	(-1.80, -0.50)
CATE	0.74	(-0.72, 2.52)	-0.10	(-0.77, 0.48)
COTE	0.14	(-0.85, 1.13)	-1.26	(-2.34, -0.49)
DCCO	1.81	(0.94, 2.85)	-0.08	(-0.35, 0.17)
FOTE	1.30	(0.03, 2.98)	-0.89	(-1.69, -0.28)
GBHE	0.65	(-0.35, 1.91)	-0.01	(-0.52, 0.38)
GREG	-0.59	(-1.77, 0.58)	-0.61	(-1.56, 0.13)
HERG	0.90	(0.48, 1.35)	0.62	(0.35, 0.93)
RBGU	0.91	(-0.66, 2.62)	-0.53	(-1.89, 0.35)

Table 3. Posterior means and 95% credible intervals for parameters measuring the effect of developed land area on site colonization probability for Great Lakes colonial waterbirds. Developed land area was measured as the proportion of area within 5 km of a potential colony site that was classified as developed land. A one-unit increase in proportion of developed land area in the model was equivalent to adding 0.19 to the actual proportion of developed land area. See “Methods” for species name abbreviations.

Species	Posterior mean	95% credible interval
BCNH	0.25	(-0.25, 0.68)
BLTE	-1.74	(-2.79, -0.96)
CATE	-0.68	(-3.03, 0.43)
COTE	0.25	(-0.08, 0.57)
DCCO	-0.02	(-0.39, 0.32)
FOTE	-1.00	(-2.56, -0.11)
GBHE	-0.24	(-0.90, 0.27)
GREG	0.24	(-0.22, 0.65)
HERG	0.23	(0.06, 0.41)
RBGU	2.62	(1.31, 4.76)

Table 4. Posterior means and 95% credible intervals for parameters measuring the effect of historical nest abundance on colony persistence probability for Great Lakes colonial waterbirds. A one-unit increase in historical nest abundance in the model is equivalent to an additional 923 nests observed in the previous census period. See “Methods” for species name abbreviations.

Species	Posterior mean	95% credible interval
BCNH	11.87	(-0.21, 27.76)
BLTE	29.21	(16.58, 42.00)
CATE	4.01	(-5.65, 21.85)
COTE	18.94	(6.35, 32.78)
DCCO	17.34	(4.04, 32.87)
FOTE	8.60	(-2.67, 25.35)
GBHE	8.68	(0.43, 21.70)
GREG	10.22	(-1.93, 27.05)
HERG	26.01	(18.83, 33.83)
RBGU	11.50	(2.13, 24.04)

Table 5. Posterior means and 95% credible intervals for parameters measuring the effects of bare nesting substrate and isolation from human access on colony persistence probability for Great Lakes colonial waterbirds. A one-unit increase in distance from human access points (roads, boat launches, etc.) in the model is equivalent to an 8.7 km increase in distance on the ground. See “Methods” for species name abbreviations.

Species	Bare substrate		Distance from human access points	
	Posterior mean	95% credible interval	Posterior mean	95% credible interval
BCNH	0.17	(-1.48, 1.94)	0.13	(-0.35, 0.69)
BLTE	0.32	(-0.59, 1.56)	0.16	(-0.24, 0.65)
CATE	-0.04	(-1.72, 1.21)	0.17	(-0.21, 0.72)
COTE	0.25	(-0.59, 1.31)	0.09	(-0.48, 0.54)
DCCO	0.01	(-1.17, 0.95)	0.13	(-0.30, 0.63)
FOTE	0.32	(-0.95, 2.17)	0.07	(-0.64, 0.57)
GBHE	-0.03	(-1.33, 1.02)	0.13	(-0.24, 0.58)
GREG	-0.06	(-2.36, 1.43)	0.21	(-0.21, 0.89)
HERG	0.20	(-0.24, 0.65)	0.17	(-0.02, 0.39)
RBGU	0.23	(-1.16, 2.00)	0.03	(-0.68, 0.46)

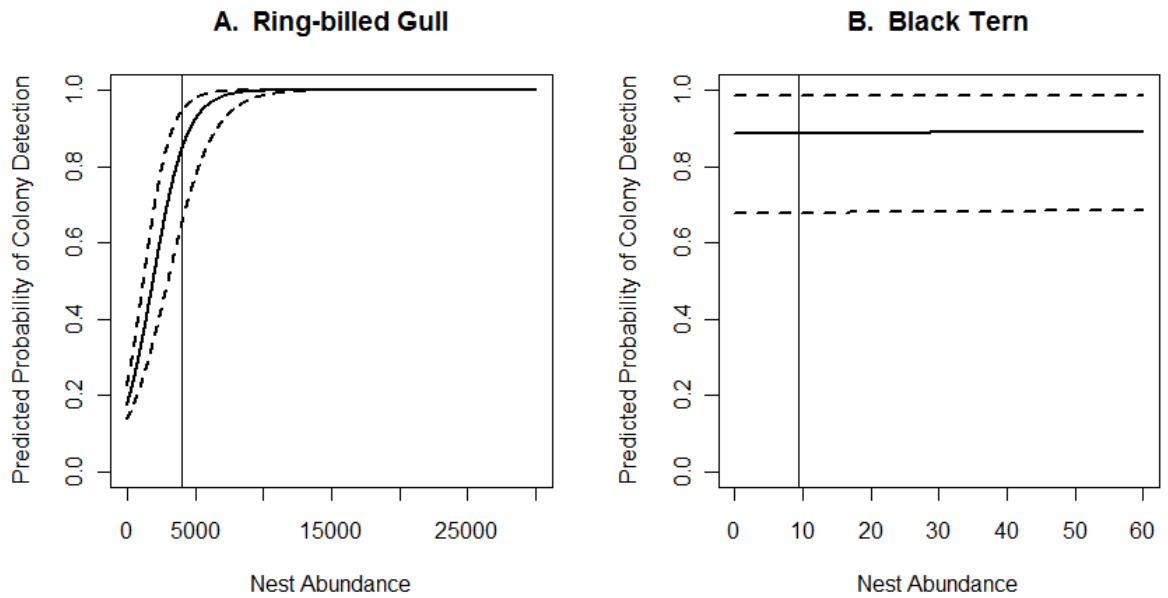


Fig. 1. Predicted probability of colony detection as a function of nest abundance for Ring-billed Gulls (*Larus delawarensis*) and Black Terns (*Chlidonias niger*). Dotted lines show 95% credible intervals. Vertical lines indicate average colony size for the species.

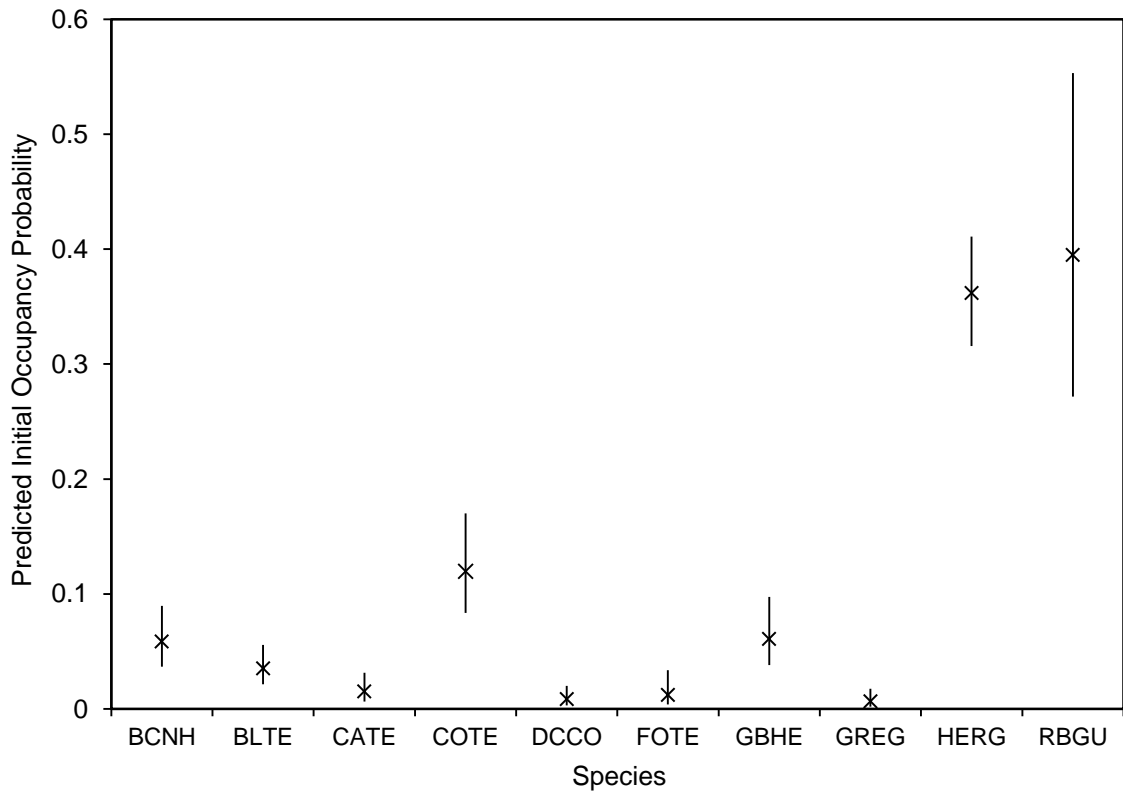


Fig. 2. Estimated initial occupancy probability of potential waterbird colony sites by species. Cross-marks show the mean of the posterior distribution and line length for each species indicates the 95% credible interval. For species name abbreviations, see Methods.

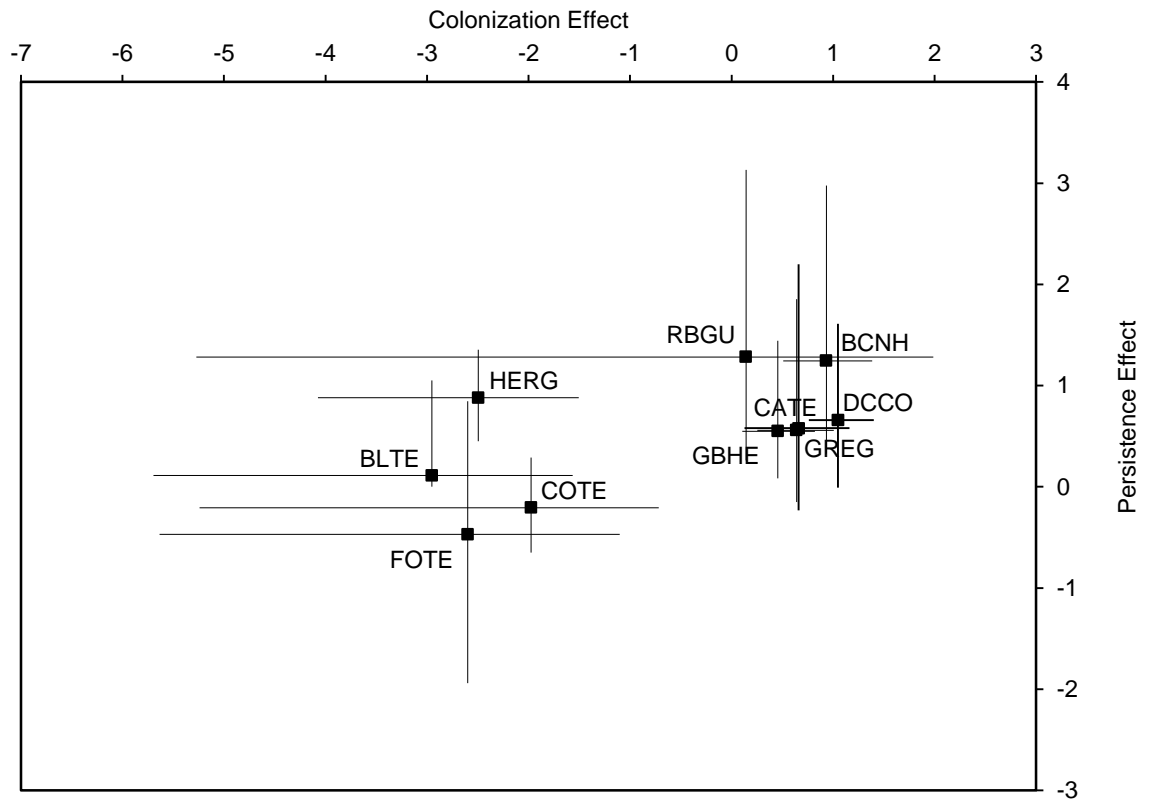


Fig. 3. Means and 95% credible intervals for posterior distributions describing the effect of species richness on colonization and persistence probabilities. For species name abbreviations, see Methods.

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## APPENDIX 2: SPATIAL DATA SOURCES

### BOAT ACCESS POINTS

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### APPENDIX 3: MODEL SPECIFICATION IN WINBUGS LANGUAGE

```
#VARIABLE NAME ABBREVIATIONS:

#sr = number of other species present

#abs = nest abundance, standardized

#dec = declining population trend (1 if true, 0 if false)

#bare = nesting substrate is not vegetated (1 if true, 0 if
      false)

#access.st = distance to human access point, standardized

#flood = site is susceptible to inundation (1 if ture, 0 if
      false)

#island = site is located on an island (1 if true, 0 if false)

#shore.st = distance to Great Lakes shoreline, standardized

#inc = increasing population trend (1 if true, 0 if false)

#LULC = proportion of area within 5km radius of colony site that
      is developed land, standardized

model{

#OCCUPANCY SUB-MODEL

for(species in 1:spp){

  logit(psi[species])<-u1[species]

for(site in 1:sites){

  z[species,site,1]~dbern(psi[species])

for(year in 2:years){

  z[species,site,year]~dbern(pi[species,site,year])
```

```

pi[species,site,year]<-phi[species,site,year]*
  z[species,site,year-1]+gamma[species,site,year]*(1-
  z[species,site,year-1])
logit(phi[species,site,year])<-b0[location[site]]+b1[species]*
  sr[species,site,year-1]+b2[species]*abs[species,site,year-
  1]+b3*dec[species,year]+b4[species]*bare[species,site,year-
  1]+b5[species]*access.st[site]+b6*flood[site]
logit(gamma[species,site,year])<-g0[species]+g1[species]*
  sr[species,site,year-1]+g2[species]*island[site]+
  g3[species]*island[site]*shore.st[site]+g4*
  inc[species,year]+g5[species]*LULC[site,year]
}}
#DETECTION SUB-MODEL
for(species in 1:spp){
for(site in 1:sites){
for(year in 1:years){
  y[species,site,year]~dbin(x[species,site,year],J[species,site,
  year])
  x[species,site,year]<-p[species,site,year]*
  z[species,site,year]
  logit(p[species,site,year])<-a0[species]+a1*
  abs[species,site,year]
}}
#PRIORS
  b3~dnorm(0,0.4)

```

```

b6~dnorm(0,0.4)
g4~dnorm(0,0.4)
a1~dnorm(0,0.4)
for(species in 1:spp){
  b1[species]~dnorm(mu.b1,tau.b1)
  b2[species]~dnorm(mu.b2,tau.b2)
  b4[species]~dnorm(mu.b4,tau.b4)
  b5[species]~dnorm(mu.b5,tau.b5)
  g0[species]~dnorm(mu.g0,tau.g0)
  g1[species]~dnorm(mu.g1,tau.g1)
  g2[species]~dnorm(mu.g2,tau.g2)
  g3[species]~dnorm(mu.g3,tau.g3)
  g5[species]~dnorm(mu.g5,tau.g5)
  a0[species]~dnorm(mu.a0,tau.a0)
  u1[species]~dnorm(mu.u1,tau.u1)
}
mu.b1~dnorm(0,0.4)
sigma.b1~dunif(0,10)
tau.b1<-pow(sigma.b1,-2)
mu.b2~dnorm(0,0.4)
sigma.b2~dunif(0,10)
tau.b2<-pow(sigma.b2,-2)
mu.b4~dnorm(0,0.4)
sigma.b4~dunif(0,10)
tau.b4<-pow(sigma.b4,-2)

```



```
mu.b5~dnorm(0,0.4)
sigma.b5~dunif(0,10)
tau.b5<-pow(sigma.b5,-2)
mu.g0~dnorm(0,0.4)
sigma.g0~dunif(0,10)
tau.g0<-pow(sigma.g0,-2)
mu.g1~dnorm(0,0.4)
sigma.g1~dunif(0,10)
tau.g1<-pow(sigma.g1,-2)
mu.g2~dnorm(0,0.4)
sigma.g2~dunif(0,10)
tau.g2<-pow(sigma.g2,-2)
mu.g3~dnorm(0,0.4)
sigma.g3~dunif(0,10)
tau.g3<-pow(sigma.g3,-2)
mu.g5~dnorm(0,0.4)
sigma.g5~dunif(0,10)
tau.g5<-pow(sigma.g5,-2)
mu.a0~dnorm(0,0.4)
sigma.a0~dunif(0,10)
tau.a0<-pow(sigma.a0,-2)
mu.u1~dnorm(0,0.4)
sigma.u1~dunif(0,10)
tau.u1<-pow(sigma.u1,-2)
```

```
for(i in 1:locations){  
  b0[i]~dnorm(0,tau.b.loc)  
}  
  
tau.b.loc<-pow(sigma.b.loc,-2)  
sigma.b.loc~dunif(0,10)  
}  
  
# in dataset, spp = 10, sites = 659, years = 4, locations = 8
```