



## Characteristics of double-crested cormorant colonies in the U.S. Great Lakes island landscape

Linda R. Wires\*, Francesca J. Cuthbert

University of Minnesota, Department Fisheries, Wildlife & Conservation Biology, 200 Hodson Hall, 1980 Folwell Ave., St. Paul, MN 55108-6124, USA

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### ABSTRACT

The Great Lakes form the largest freshwater island system in the world and provide breeding habitat for a large proportion of the continental population of double-crested cormorants (*Phalacrocorax auritus*). Here, cormorants have a high profile due to conflicts with humans; by 2007, most active (64%) breeding sites in U.S. waters were managed. This study used data from the U.S. Great Lakes Colonial Waterbird Database and The Nature Conservancy's Great Lakes Island GIS database to identify important features of breeding sites in the U.S. Great Lakes and broaden understanding of cormorant presence at the island-landscape scale. Islands 0.5–10 ha were used more frequently than expected, and most sites had remoteness values of  $\leq 3$  km. Colony size was positively correlated with years occupied and large colonies ( $>1000$  pairs) developed primarily (95%) on island sites  $>1.0$  ha. Sites supporting large colonies were more remote than those supporting smaller colonies. Presence of other colonial waterbird species, especially Herring Gulls (*Larus argentatus*), also characterized cormorant sites. Islands used by cormorants comprised a small proportion ( $n=90$ , 3%) of the U.S. Great Lakes island resource, and  $<1\%$  of the total island area. Certain characteristics of breeding sites (e.g., small islands, proximity to mainland) may increase negative attitudes about cormorants. To understand cormorant impacts to island resources (e.g., vegetation; other colonial waterbird species), we suggest cormorant presence in the Great Lakes be considered in the broader context of island science, conservation and known threats, and at a landscape scale.

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### Introduction

In North America, five main breeding zones have been described for the double-crested cormorant (*Phalacrocorax auritus*, hereafter: cormorant) (Hatch and Weseloh, 1999). Originally, zones were thought to correspond largely with distribution of subspecies (Palmer, 1962; Johnsgard, 1993), but more recent work suggests geographic distance, rather than discrete subspecific breaks between regions, distinguishes populations in the conterminous U.S. and Canada (Mercer, 2008). The breeding population in the Interior Region is the largest and most widespread, spanning the prairie provinces of Canada, the Great Lakes and southwestern Quebec (Wires and Cuthbert, 2006). The Great Lakes comprise the largest freshwater island system in the world (Vigmostad, 1999) and represent a particularly important core area; approximately 52% of the Interior Region's breeding pairs nested in the Great Lakes in the late 1990s (Wires and Cuthbert, 2006). Although cormorants were nearly extirpated from this region during the DDT-era (1940s–1970s), reaching a low of 89 pairs at eight sites in 1970 (Weseloh et al., 1995), over the last thirty years the Great Lakes have become one of

the most significant breeding areas within the species' continental range (Wires et al., 2010). Since the early 1970s, 260 sites, mostly islands, have been used by nesting cormorants; in 2000, the Great Lakes population was estimated at 115,000 pairs (Weseloh et al., 2002). In addition, cormorants have experienced high rates of productivity in this area since their resurgence (Weseloh and Ewins, 1994; Weseloh et al., 1995).

As cormorants have become more abundant in the Great Lakes, various aspects of their behavior and biology have been studied in detail (e.g., Weseloh et al., 1995; Neuman et al., 1997; Cuthbert et al., 2002; Hebert et al., 2005; Seefelt, 2005; Coleman and Richmond, 2007). However, little work has been conducted to characterize breeding sites used by cormorants in this region. With the exception of Trexel (2002), who studied colony sites in northern lakes Huron and Michigan, no similar work has been conducted at a regional scale. In addition to expanding knowledge of the nesting requirements of cormorants, such information is important to predict site use patterns and biodiversity impacts, identify regionally important colony locations and provide context for cormorant management.

Because the population reached a low point at approximately the same time Great Lakes-wide colonial waterbird survey efforts were jointly initiated by the Canadian Wildlife Service (CWS) and the U.S. Fish and Wildlife Service (USFWS) (Blokpoe, 1977; Blokpoe and McKeating, 1978; Scharf, 1978; Blokpoe et al., 1980; Weseloh et al.,

\* Corresponding author.

E-mail address: [Wires001@umn.edu](mailto:Wires001@umn.edu) (L.R. Wires).

1986), a unique database exists that documents the spectrum of sites chosen for nesting since re-colonization of cormorants in the Great Lakes started. The purpose of this paper is to characterize features of nesting sites used by cormorants in the U.S. portion of the Great Lakes from the initial period of population recovery in the 1970s through the mid-2000s when cormorant control became widespread on the U.S. Great Lakes. We summarize physical attributes of cormorant nesting locations including type and area of site, distance of colony from mainland and its remoteness, nesting substrate, presence of other nesting colonial waterbird species, and cormorant colony size. To broaden understanding of cormorant presence within the Great Lakes landscape, this information is also presented in the context of the Great Lakes island resource.

## Study area

The study area includes the U.S. portions of the five Great Lakes (lakes Superior, Michigan, Huron, Erie, and Ontario) and their connecting rivers (St. Marys, St. Clair, Detroit, and Niagara) from Pigeon Point, Minnesota (at the U.S.–Canadian border) to Massena, New York, along the St. Lawrence River. The area encompasses part or all of eight states (Minnesota, Wisconsin, Illinois, Indiana, Michigan, Ohio, Pennsylvania and New York). Thousands of islands are dispersed among the lakes and rivers, and range in size and character from small rocky islets to large forested landscapes encompassing thousands of hectares (Vigmostad 1999). Cormorants utilize a wide variety of islands across this landscape for nesting. Precambrian islands of basalt and granite dominate the northern shores of Lake Superior, Lake Huron and the St. Lawrence River. The islands of Lake Superior's southern shore are comprised of Precambrian and Cambrian sandstone formations. Northern Lake Michigan and lakes Huron, Erie, and Ontario, are characterized by limestone and dolomite islands. Scattered throughout the Great Lakes are islands composed of glacial deposits, and Deltaic islands are locally found at mouths of rivers, especially the St. Clair River (Crispin, 1999). Water level fluctuations occur seasonally and over both the short- and long-term. Short-term fluctuations due to high winds, storms and ice jams occur over hours or days and can be dramatic. Long-term fluctuations due to climate variability occur over years and can also be pronounced. Although water levels are regulated to some extent, the effects of these efforts are limited and minor relative to natural factors (USACE and GLC, 1999).

## Methods

### Colony sites

We chose the thirty year time period between 1977 and 2007 to characterize sites selected by cormorants in U.S. waters. Our decision was based on the assumption that cormorants selected most sites during this period relatively free from human disturbance. To identify sites used during this period we compiled data from the U.S. Great Lakes Colonial Waterbird Database (GLCWBD) which includes data from: 1) decadal survey efforts reported in Scharf, 1978; Scharf and Shugart, 1998; Cuthbert et al., 2010; 2) unpublished data from surveys conducted between 2000 and 2007, by F.J. Cuthbert and D.V. Weseloh; and 3) agencies monitoring cormorants in the study area in years not included in the decadal census. Breeding sites were categorized as islands, island-like structures and mainland sites. Islands included all naturally occurring and human-created land masses (e.g., dredge spoil islands) surrounded by water, and ranged in size and character from small bare rocks, shoals and sand spits, to large and densely forested areas. Sites categorized as island-like structures (e.g., navigation aids, piers, weirs, cribs and shipwrecks) were surrounded by water and separate from the mainland. As such, these sites were assumed to function essentially as islands in their

potential to provide nesting habitat for cormorants. Mainland sites included locations on the mainland that were within 1 km of the Great Lakes shoreline, the area within which census efforts were conducted during the Great Lakes Colonial Waterbird Survey.

### Proportion of U.S. Great Lakes islands and maximum island area used

To determine the proportion of U.S. Great Lakes islands used by cormorants during the time of our study, we divided the total number of islands occupied by cormorants by the total number of islands ( $N=3085$ ) reported in The Nature Conservancy's (TNC) GIS island database (TNC, 2006). Islands in TNC's database included natural and human-created landmasses, such as dredge spoil islands, but not island-like structures or mainland sites. We were not able to determine total island area occupied as this requires detailed spatial information on cormorant distribution for every island used. However, we estimated the maximum proportion of total U.S. Great Lakes island area occupied by cormorants by dividing the combined area of all U.S. Great Lakes islands used by cormorants by total area of U.S. Great Lakes islands (261,372 ha) identified by TNC (2006).

### Colony site size

For most islands used by cormorants, we used ArcMap to determine island size by overlaying point locations of cormorant sites onto the island polygon files created by TNC. For a small number of islands, we obtained area information from other sources (e.g., the Internet; published literature). For a few islands that lacked area measurements, we estimated island sizes by identifying them on nautical charts and comparing them to islands of known sizes. Sizes of island-like structures were not available, so to estimate this variable, we examined and compared these sites to small islands of known size used by cormorants, and assigned an estimate of 0.20 ha to each island-like structure. Sizes of mainland sites were not provided because these sites are not isolated and do not have discrete boundaries. To identify island size most frequently used, we developed five island-size range categories (0.01–0.5, 0.51–1.0, 1.01–3.0, 3.01–10, and >10 ha) based on island sizes used by nesting cormorants and identified modal range. To determine if cormorants use island sizes randomly based on their availability in the landscape, we compared island sizes used by cormorants to those available using a chi-squared test.

### Distance from mainland and island remoteness

To describe island remoteness we used the Google Earth distance measuring tool to estimate the distance of a colony on an island or on an island-like structure to the nearest point of mainland. However, if an island developed by humans or known to support mammalian predators was closer than the mainland, we also measured distance to this island. Such islands varied greatly in size but were relatively large (89.8–50,349 ha). When two measurements were taken, remoteness was based on smallest distance. To identify the distance from mainland and remoteness of islands which occurred most frequently, we developed six categories of distance (0.0–1.0, 1.01–2.0, 2.01–3.0, 3.01–5.0, 5.01–10, and >10 km) based on measured distance/remoteness of islands and identified modal distance and remoteness.

### Nesting substrate

Data on substrate used for nesting by cormorants were obtained from the GLCWBD and from individuals monitoring cormorants. Because we were interested in impacts to vegetation and habitat of other colonial species, nest substrate was broadly classified based on ground- or tree-nesting. Ground substrate categories consisted of rock, sand, soil, or herbaceous vegetation, and tree categories included

trees and or shrubs. Additionally, some sites (e.g., island-like structures) did not fit well into either ground or tree categories. These sites were categorized as “other.”

#### Presence of co-nesting colonial waterbird species

To determine species composition and most frequent nesting associates at cormorant colonies, data on presence of co-nesting colonial waterbird species at sites used by cormorants were obtained from the GLCWBD and from individuals monitoring cormorants. Specifically we determined what percent of cormorant sites was occupied by each co-nesting colonial waterbird species. We also used data from all census periods to examine history of site use by other nesting colonial waterbird species and determined the species that typically occupied each site prior to its colonization by cormorants.

#### Colony size

Data on colony sizes from the mid-1970s to 2007 were summarized from the U.S. GLCWBD. Because colony sizes change over time, we examined all available census data for each site to characterize a colony's size. To determine number of years occupied, we first reviewed census records to identify year of site colonization, defined as the first year cormorants were known to breed at or return to a site since their near extirpation in the 1970s. If the year of colonization was not known, we identified the year the first breeding record was obtained. For sites that were monitored yearly since colonization or first breeding record, actual number of years occupied was available. For sites that were monitored intermittently over a long period and consistently active, number of years occupied was assumed to have been years since colonization or first documented use. Based on colony sizes observed in the database, four size ranges

were identified to characterize colonies: 1–100 pairs (small), 101–500 pairs (moderate), 501–1000 pairs (moderately large), and >1000 pairs (large). For colonies with data that fell equally within two size ranges, the most recent trend information was also considered. If sites were occupied for  $\leq$  five years or inadequately sampled over time, sites were not characterized in terms of size. Additionally, colony size data for colonies subjected to population control were eliminated after the year following initiation of control. However, we included data for colonies that were not managed, but were near colonies experiencing control. Correlation analysis (Pearson's Correlation Coefficient) was used to determine relationships between colony size and length of time occupied, area, distance and remoteness.

## Results

#### Proportion of islands and maximum island areas used

Between 1977 and 2007, cormorants were reported as a nesting species at 100 sites in the U.S. Great Lakes (Fig. 1); of these, 90 (90%) were island sites, while the remaining 10% were island-like structures and mainland sites (Table 1). The percent of island sites represents a very small proportion of the total island resource; cormorants have occupied approximately 3% of Great Lakes islands over the 30 year study period (Table 2). In terms of island area, the combined area of all islands used by cormorants was 2460 ha or approximately 1% of Great Lakes island area (Table 2). This figure overestimates the actual area used by cormorants as it represents maximum island area used; cormorants did not occupy the entire island area available on any island where they nested.

Cormorants utilized the greatest number of islands in Lake Michigan, which has the largest island area of the U.S. portion of the five Great Lakes and their connecting channels (Table 2). Over the

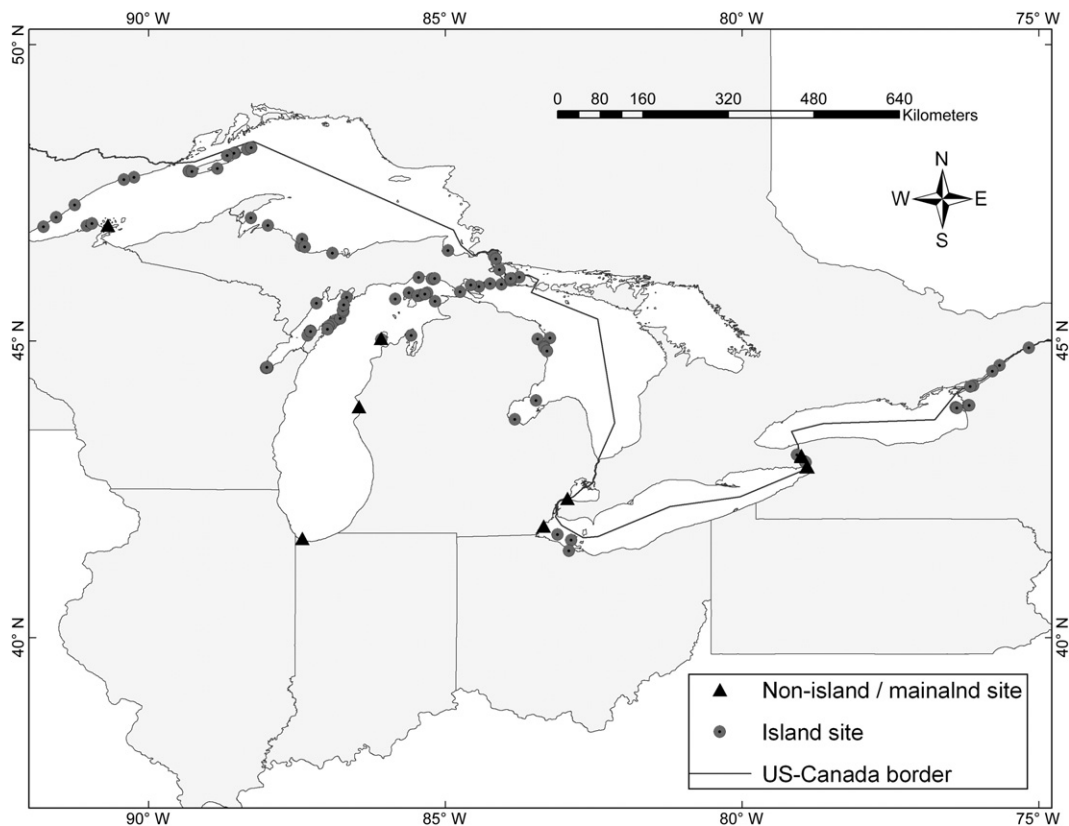


Fig. 1. Double-crested cormorant colony sites in the U.S. Great Lakes, 1977–2007.

**Table 1**

Attributes of sites used in the U.S. Great Lakes by nesting double-crested cormorants (DCCO), 1970s–2007. Archipelagos: AP = Apostle Island; BI = Bass Island; BV = Beaver Island; IR = Isle Royale; LC = Les Cheneaux Islands. Co-occurring species: AWPE = American white pelican; BCNH = black-crowned night-heron; CAEG = cattle egret; CATE = Caspian tern; COTE = common tern; GBBG = great black-backed gull; GBHE = great blue heron; GREG = great egret; HERG = herring gull; LBHE = little blue heron; RBGU = ring-billed gull; SNEG = snowy egret. Data from U.S. Great Lakes Colonial Waterbird Database.

Site name [archipelago]	State	Land type	Year colonized or first nest record <sup>a</sup>	Last year known active	Years known or assumed active	Area (ha)	Distance to mainland/ remote-ness <sup>b</sup>	Nesting substrate	Co-nesting species	Size range category (pairs)	Legal DCCO control
<i>Lake Erie</i>											
West Sister Island	OH	I	1992	2007	16	27.49	13.57	Tree	HERG, BCNH, GBHE, GREG, CAEG, LBHE, SNEG	>1000	Yes
Green Island [BI]	OH	I	2004	2007	4	6.48	6.77	Tree	HERG, BCNH, GBHE, GREG	NA <sup>c</sup>	Yes
Turning Point Island	OH	I	1999	2007	8	2.70	2.37	Tree	HERG, BCNH, GBHE, GREG, CAEG	101–500	Yes
Detroit Edison Power Donnelly's Wall (Buffalo Harbor)	MI NY	M NI	1998 2002	1998 2006	1 5	NA <sup>d</sup> 0.2	NA <sup>d</sup> 0.53	Tree Ground	HERG, RBGU HERG, RBGU	NA <sup>c, e</sup> NA <sup>f</sup>	No Yes
Reef Light House	NY	NI	1995	2007	8	0.2	1.45	Other	COTE/NONE	101–500	Yes
<i>Lake Huron</i>											
Little Saddlebag Island [LC]	MI	I	1988	2007	20	0.52	0.74	Tree, ground	HERG	501–1000	Yes
Crow Island [LC]	MI	I	1989	2007	19	1.12	0.96	Tree	HERG, RBGU, GBHE	101–500	Yes
Goose Island [LC]	MI	I	1987	2005	19	7.36	3.01	Trees	HERG, RBGU, BCNH, GBHE	>1000	Yes
St. Martin Shoal [LC]	MI	I	1981	2007	27	1.25	3.6	Ground	HERG, RBGU	>1000	Yes
Gull Island	MI	I	1985	2007	23	5.24	3.72	Tree	HERG, GBBG, BCNH, GBHE	>1000	Yes
Grass Island	MI	I	1997	2007	11	1.82	0.85	Tree	HERG, RBGU, BCNH, GBHE, GREG	101–500	Yes
Scarecrow Island	MI	I	1980	2007	28	2.92	2.9	Ground, tree	HERG, GBBG, CATE, COTE, BCNH, GBHE	>1000	Yes
Bird Island	MI	I	1989	2007	19	2.34	0.65	Ground, tree	HERG, RBGU, BCNH, GBHE	501–1000	Yes
Black River Island	MI	I	1980	1989	NA <sup>g</sup>	0.50	0.38	Tree	HERG	NA <sup>g</sup>	No
Little Charity Island	MI	I	1996	2007	12	6.04	10.15/3.23	Tree, ground	HERG, CATE, BCNH, GBHE, GREG	>1000	No
Saginaw Combined Disposal Facility	MI	I	2004	2007	4	104.48	3.22	Tree	HERG, RBGU, BCNH, GBHE, GREG, CATE, COTE	NA <sup>c</sup>	No
Green Island [LC]	MI	I	1995	2007	13	4.27	0.21	Tree, ground	HERG, RBGU, BCNH, GREG	101–500	Yes
<i>Lake Michigan</i>											
Epoufette Island	MI	I	1992	1999	8	2.20	0.11	Tree	HERG, BCNH, GBHE	NA <sup>g</sup>	No
Naubinway Island	MI	I	1984	2007	24	0.36	0.99	Ground	HERG, RBGU	501–1000	Yes
Epoufette Shoal	MI	I	1989	1989	1	0.56	0.4	Ground	HERG, RBGU	NA <sup>c</sup>	No
Davenport Creek Shoal (Paquin Island)	MI	I	1997	2007	11	3.76	0.1	Ground	HERG, RBGU	101–500	Yes
Snake Island, Bay de Noc	MI	I	1981	2007	24	3.41	0.85	Tree, ground	HERG, RBGU	>1000	Yes
Fisherman's Island	MI	I	1984	2007	24	0.44	0.96	Ground, tree	HERG, RBGU, COTE	501–1000	Yes
Hat Island, Green Bay	WI	I	1981	2007	22	1.85	4	Tree, ground	HERG, RBGU, BCNH, AWPE	>1000	Yes
Jack Island	WI	I	1981	2007	27	2.31	2.16	Ground	HERG, BCNH	>1000	Yes
Little Strawberry Island	WI	I	1993	2005	NA <sup>g</sup>	2.93	2.22	Tree	HERG	NA <sup>g</sup>	No
Hog Island	WI	I	1988	2007	NA <sup>g</sup>	0.76	0.65	Tree	HERG, GBHE, BCNH	NA <sup>g</sup>	Yes
Pilot Island	WI	I	1992	2007	16	1.29	3.98/1.81	Tree	HERG, RBGU, BCNH, GBHE	>1000	No
Fish Island	WI	I	1976	1997	18	0.70	19.39/5.67	Ground	HERG	1–100	No
Big Gull Island	MI	I	1980	2007	16	7.12	12.11/2.74	Tree, ground	HERG, BCNH, GBHE	>1000	Yes
Little Gull Island	MI	I	1980	2007	28	3.45	13.52/3.15	Ground, tree	HERG, BCNH, GBHE, AWPE	>1000	Yes
Gravelly Island	MI	I	1977	1989	13	1.56	11.96 / 3.01	Ground	HERG, RBGU, GBBG, CATE	1–100	No
Spider Island	WI	I	1980	2007	28	6.26	0.9/	Ground	HERG, GBBG	>1000	No
Gravel Island	WI	I	1978	1989	12	0.42	1.06	Ground	HERG	1–100	No
Rocky Island	MI	I	1989	2007	9	9.48	2.76	Tree	HERG, RBGU, BCNH, GBHE	101–500	No
Little Spider Island	WI	I	1980	1989	NA <sup>g</sup>	0.40	2.76	Ground	HERG	NA <sup>g</sup>	No
Bellow Island	MI	I	1989	2007	19	1.65	2.12	Tree, ground	HERG, RBGU, CATE	>1000	Yes
Gull Island [BV]	MI	I	1981	2007	27	88.91	24.04/10.75	Ground, tree	HERG, RBGU, CATE, BCNH	>1000	Yes
Whiskey Island [BV]	MI	I	1997	1998	2	32.49	17.27/6.28	Ground, tree	HERG	NA <sup>c</sup>	No
Pismire Island [BV]	MI	I	1984	2007	24	0.71	27.25/1.09	Ground	HERG, RBGU	501–1000	Yes
Grape Islands (East and West) [BV]	MI	I	1988	2001	14	2.83	28.1/1.8	Ground, tree	HERG, RBGU, GBHE	>1000	No

(continued on next page)

Table 1 (continued)

Site name [archipelago]	State	Land type	Year colonized or first nest record <sup>a</sup>	Last year known active	Years known or assumed active	Area (ha)	Distance to mainland/ remote-ness <sup>b</sup>	Nesting substrate	Co-nesting species	Size range category (pairs)	Legal DCCO control
<i>Lake Michigan</i>											
Hat Island [BV]	MI	I	1982	2007	26	5.41	23.2 4.02	Ground, tree	HERG, RBGU, CATE, BCNH, GBHE	>1000	Yes
Ile aux Galets	MI	I	2000	2007	8	4.95	9.15	Ground	HERG, RBGU, CATE	501–1000	Yes
Snake Island [BV]	MI	I	1993	2006	NA <sup>g</sup>	1.47	26.3/0.23	Ground	HERG, RBGU, COTE	1–100	No
Timms Island [BV]	MI	I	1997	2000	4	1.48	27.63/0.49	Tree	HERG, RBGU	NA <sup>c</sup>	No
Cat Island Shoal	WI	I	1976	1977	2	0.40	0.38	Tree	NONE	NA <sup>c, d</sup>	No
Lone Tree Island	WI	I	1988	2007	NA <sup>g</sup>	0.50	1.91	Ground, tree	HERG, RBGU, BCNH, GREG, SNEG, AWPE	NA <sup>g</sup>	Yes
Cat Island	WI	I	1974	2007	34	0.92	1.7	Tree, ground	HERG, BCNH, GREG, AWPE, CAEG, SNEG	>1000	Yes
Inland Steel	IN	M	2004	2007	4	0.00	0	Ground	HERG, RBGU, BCNH, GREG	NA <sup>c</sup>	No
South Manitou Island	MI	I	2002	2007	6	1904.0	10.34/7.0	Tree	NONE	NA <sup>e</sup>	Yes
Morazan Shipwreck	MI	NI	1989	2007	19	0.20	11.5	Other	HERG	101–500	No
Ludington Pump Storage Breakwall	MI	NI	2006	2007	2	0.00	0.52	Ground	HERG	NA <sup>c, f</sup>	Yes
<i>Lake Ontario</i>											
Little Galloo Island	NY	I	1974	2007	34	18.10	8.47/1.8	Tree, ground	HERG, RBGU, GBBG, CATE, BCNH, CAEG	>1000	Yes
Gull Island	NY	I	1994 or earlier	2007	NA <sup>g</sup>	0.83	3.01	Tree, ground	HERG, GBBG, BCNH	NA <sup>f</sup>	Yes
Bass Island	NY	I	1994 or earlier	2007	NA <sup>g</sup>	2.01	2.67	Tree	RBGU, BCNH	NA <sup>f</sup>	Yes
Calf Island	NY	I	1997	2004 or later	NA	9.57	6.03/3.75	Tree	BCNH	NA <sup>c, f</sup>	Yes
<i>Lake Superior</i>											
Passage North [IR]	MI	I	2007	2007	1	0.50	25.32/5.78	Ground	HERG	NA <sup>c</sup>	No
Gull Two [IR]	MI	I	1998	1998	1	0.46	26.42/14.2	Ground	HERG, RBGU	NA <sup>c</sup>	No
Steamboat Island [IR]	MI	I	1989	2007	19	0.49	24.54 / 2.12	Ground	HERG	101–500	No
Net Island [IR]	MI	I	1997	2006	10	2.28	24.35 / 1.93	Ground, tree	HERG, GBHE	101–500	No
Amygdaloid South Island [IR]	MI	I	1989	2007	19	0.50	23.81 / 1.5	Ground	HERG	1–100	No
Five Mile Rock (Guano Rock)	MN	I	1997	2007	11	0.10	1.15	Ground	HERG	1–100	No
MN DNR 37	MN	I	1997	1998	2	2.03	0.92/	Ground	HERG	NA <sup>c</sup>	No
MN DNR 79	MN	I	1989	1989	1	3.91	0.27	Ground	HERG	NA <sup>c</sup>	No
Rock N. Mining Facility	MN	I	2007	2007	1	0.20	0.32	Ground	HERG, RBGU	NA <sup>c</sup>	No
Traverse Island	MI	I	1989	1997	9	32.96	3.2	Tree	HERG, GBHE	1–100	No
Rock of Ages and Rock North [IR]	MI	I	2006	2007	2	0.42	22/6.11	Ground	HERG	NA <sup>c</sup>	No
North Rock [IR]	MI	I	1997	1997	1	0.43	23.91/3.25	Ground	HERG	NA <sup>c</sup>	No
South Rock [IR]	MI	I	2007	2007	1	0.08	23.69/2.33	Ground	HERG	NA <sup>c</sup>	No
Paul Island Rocks [IR]	MI	I	1997	2007	11	0.09	42.7/5.35	Ground	HERG	1–100	No
Knife Island	MN	I	2001	2007	7	0.98	0.4	Tree	HERG	1–100	Yes
Eagle Island [AP]	WI	I	1984	2007	24	10.00	3.6	Ground, tree	HERG, GBHE	101–500	No
Gull Island [AP]	WI	I	1978	2007	30	1.27	2.02	Ground, tree	HERG	501–1000	No
Huron Island	MI	I	1989	2007	19	0.20	5.08	Ground	HERG, GBHE	1–100	No
Larus Island	MI	I	2007	2007	1	0.50	1.33	Ground	HERG	NA <sup>c</sup>	No
Granite Island	MI	I	1997	1997	1	1.01	8.95	Ground	HERG	NA <sup>c</sup>	No
Au Train Island	MI	I	1998	2006	9	42.90	1.75	Tree	HERG	1–100	No
Tahquamenon Island	MI	I	1989	2007	19	0.63	4.74	Ground	HERG, RBGU	101–500	Yes
Presque Isle Rock	MI	I	2007	2007	1	0.20	1.03	Ground	HERG	NA <sup>c</sup>	No
Round Island	MI	I	1993/94	2007	NA <sup>g</sup>	2.95	0.69	Ground, tree	BCNH, HERG, RBGU	NA <sup>e</sup>	Yes
AP Nav Aid [AP]	WI	NI	1994	2007	NA <sup>g</sup>	0.20	8.5	Ground	HERG	NA <sup>e</sup>	No
<i>Lake St. Clair</i>											
Peché Island Rear Range Light	MI	NI/M	2005	2007	3	0.20	0	Ground	NONE	NA <sup>c</sup>	No
<i>Niagara River</i>											
Goat Island	NY	I	2000	2007	8	39.02	0.28	Ground, trees	HERG, RBGU, GBBG	101–500	No
Motor Island	NY	I	1997 or earlier	2006	10	2.92	0.44	Tree	RBGU, BCNH, GBHE, GREG	1–100	Yes
Strawberry Island	NY	I	1997	2007	11	7.53	0.6	Tree	HERG, RBGU	101–500	Yes
Buckhorn Weir	NY	NI	2002	2007	6	0.00	0.14	Ground	HERG, RBGU	1–100	Yes
Buckhorn Far Crib	NY	NI	2004	2007	4	0.20	0.31	Other	COTE	NA <sup>c</sup>	No
<i>St. Lawrence River</i>											
Eagle Wings Island	NY	I	2004	2004	1	0.46	1.61	Ground	COTE	NA <sup>c, f</sup>	Yes
Blanket Island	NY	I	2001	2007	7	0.38	1.65	Tree	HERG	101–500	Yes

Table 1 (continued)

Site name [archipelago]	State	Land type	Year colonized or first nest record <sup>a</sup>	Last year known active	Years known or assumed active	Area (ha)	Distance to mainland/remote-ness <sup>b</sup>	Nesting substrate	Co-nesting species	Size range category (pairs)	Legal DCCO control
<i>St. Lawrence River</i>											
Bogardus Island	NY	I	2000	2002	3	0.26	0.64	Tree	NA	NA <sup>c</sup>	Yes
Murphy Island	NY	I	2002	2007	6	1.46	0.83	Tree	RBGU	1–100	Yes
West Crossover Island	NY	I	2001	2007	6	0.06	1.14	Ground	HERG	1–100	Yes
<i>St. Marys River</i>											
Gem Island	MI	I	1989	2007	19	0.67	0.77	Tree	HERG, GBHE	101–500	Yes
Rock Island	MI	I	1997	2007	11	0.64	0.36	Tree	HERG, BCNH, GBHE	101–500	Yes
Two Tree Island	MI	I	1998	1998	1	0.20	0.65	Tree	HERG, RBGU	NA <sup>c</sup>	No
Twin Pipe West Island	MI	I	1997	1997	1	0.34	1.81	Tree	HERG	NA <sup>c</sup>	No
Twin Pipe East Island	MI	I	1997	1997	1	0.16	2.07	Tree	HERG	NA <sup>c</sup>	No
Propeller Island	MI	I	1997	1997	1	0.25	1.55	Tree	HERG	NA <sup>c</sup>	No
Little Cass Island	MI	I	1997	2005	9	0.31	1.92	Ground	HERG, RBGU, COTE, CATE	1–100	No

<sup>a</sup> First breeding record obtained, known colonization or re-colonization since near extirpation prior to 1970.

<sup>b</sup> Remoteness value based on shortest of two distances measured from breeding site to mainland and to nearest large island, with large qualitatively defined as inhabited by humans or mammalian predators.

<sup>c</sup> Not available, site was occupied <5 years.

<sup>d</sup> Not applicable, mainland site.

<sup>e</sup> Not available, site had only one data point.

<sup>f</sup> Not available, site controlled early in development.

<sup>g</sup> Not available, site too inconsistently monitored or used.

30-year study period, cormorants nested on 10% of these islands, in addition to two island-like structures and one mainland site. Maximum island area used by cormorants represented only 0.22% of Lake Michigan’s total island area. In Lake Superior, cormorants utilized approximately 4% of islands and one island-like structure and nested on a maximum island area of 0.13% of the lake’s total island area. On Lake Huron, cormorants used <3% of the lake’s islands and did not occupy island-like structures or mainland sites. Maximum island area used represented 0.32% of Lake Huron’s total island area. The U.S. portions of lakes Ontario and Erie have much smaller numbers of islands and total island areas, and relatively few islands were used by cormorants in the U.S. portions of these lakes (Table 2). The St. Marys and St. Lawrence rivers have large numbers of islands; proportionally few (~1%) were utilized by cormorants, and maximum island area occupied in these water bodies was very small (0.02%; Table 2). The Niagara River had the highest proportion of islands utilized by cormorants (16%) but this river has relatively few islands compared to most water bodies in the study area. No islands were used by cormorants in the Detroit River or Lake St. Clair, but nesting did occur for the first time in Lake St. Clair on an island-like structure in 2005.

Table 2  
Number and area of islands used by nesting double-crested cormorants (DCCO) in each waterbody relative to island availability in the U.S. Great Lakes.

Waterbody	Number of islands	Total island area (ha)	Number of islands used by DCCO	Number of island-like structures/mainland sites used by DCCO	Maximum island area (ha) used by DCCO
Lake Superior	630	76436.674	24	1	105.09
Saint Marys River	483	18041.995	7	0	2.57
Lake Michigan	332	93872.617	32	3	2094.98
Lake Huron	493	43708.533	12	0	137.85
St. Clair River	0	0.000	0	0	0.00
Lake St. Clair	31	4456.990	0	1	0.00
Detroit River	23	2487.895	0	0	0.00
Lake Erie	153	3057.660	3	3	36.67
Niagara River	19	7505.194	3	2	49.48
Lake Ontario	105	2185.517	4	0	30.51
St. Lawrence River	816	9618.837	5	0	2.62
Total USGL islands	3085	261371.912	90	10	2459.77

Sizes of sites used by cormorants

Size of islands and island-like structures used by cormorants ranged broadly, from 0.06 to 1904 ha (Table 1). Average size of a site (excluding mainland locations) occupied was approximately 25 ha +/- 192 SD (n = 98). However, this mean is heavily skewed by nesting that occurred on three unusually large islands: South Manitow Island, a 1904 ha natural island in Lake Michigan; the Saginaw Combined Disposal Facility (CDF), a 104.48 ha human-created island used for sediment disposal in Lake Huron; and Gull Island, an 88.91 ha natural island in Lake Michigan. Only nine sites used by cormorants were >10 ha; excluding these very large sites, mean nesting location size was 1.9 ha +/- 2.4 SD (n = 89).

The majority (73%) of islands and island-like structures used were <3.0 ha in size, and the modal size range was 0.01–0.5 ha (Fig. 2). Because most islands (72%) in the U.S. Great Lakes are small (<=0.5 ha), and large islands (>10 ha) are not common in the study area (Fig. 2), there may be an intrinsic bias in the dataset. However, cormorants did not use island sizes proportional to their availability (X<sup>2</sup> = 101.2, 4 df, P < 0.001). Islands <=0.5 ha were used less frequently than expected, while islands in the size ranges 0.51–1.0, 1.01–3.0, and

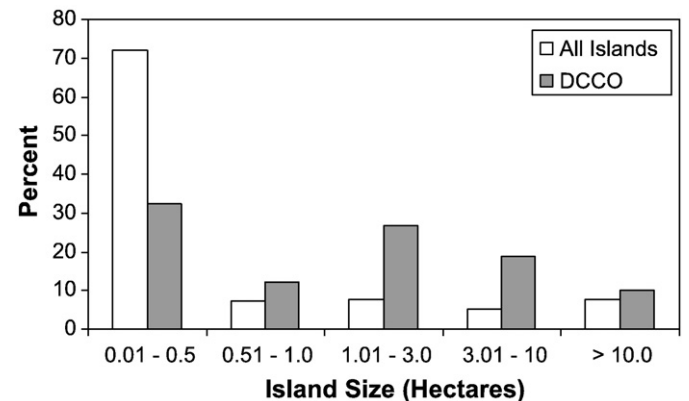


Fig. 2. Island sizes used by double-crested cormorants (DCCO) relative to islands available in the U.S. Great Lakes, 1977–2007.

3.01–10 ha, were used more frequently than expected. Islands > 10 ha appeared to be used in proportion to availability.

*Distance from mainland and remoteness*

Distance of islands and island-like structures from the mainland used by cormorants ranged from 0.1 km to sites as far away as 42.7 km, and averaged 6.8 km +/- 9.4 SD (n = 98); site remoteness ranged from 0.1 km to 14.2 km, and averaged 2.4 km +/- 2.6 SD (n = 98) (Table 1). Modal distance and remoteness were both ≤ 1 km; more than half (58%) of the sites were ≤ 3 km from the mainland, and 72% had remoteness values of ≤ 3 km (Fig. 3). Of the 24 sites that were > 10 km from the mainland, 23 were less remote than their distance to mainland estimates suggested; only 3 were more remote than 10 km (Table 1 and Fig. 3). Most sites (67%) far from the mainland (> 10 km) were associated with archipelagoes; of these, 56% were part of the Isle Royale archipelago in Lake Superior, while the remaining 44% were part of the Beaver Island archipelago in Lake Michigan. Additionally, large sites (> 10 ha) used by cormorants were more remote (n = 9, mean = 5.3 +/- 4.5 SD) than smaller ones (≤ 10 ha) (n = 89, mean = 2.1 +/- 2.2 SD).

*Substrate used for nesting*

Nesting substrate was identified for all sites (Table 1). The majority of sites were characterized by ground-nesting on substrates of rock, sand, or soil, with at least some portion of nests on the ground at 61% of the 100 sites used. Tree-nesting was also observed frequently, with some portion of birds nesting in trees at 58% of the 100 sites used. Birds often utilized both ground and trees at individual sites (26%). At eight sites (8%), cormorants nested on island-like structures on substrates classified as “other” because they did not match ground- or tree-nesting categories. At island colonies in Lake Erie, and the Niagara and St. Marys rivers, trees were used almost exclusively (Table 1, Fig. 4). In lakes Huron, Michigan and Ontario, and on the St. Lawrence River, tree-nesting was recorded on ≥ 50% of islands. Lake Superior had the lowest proportion of islands with tree-nesting birds, only 28%.

*Presence of co-nesting colonial waterbird species*

Cormorants rarely nested as a single species; over the course of the survey period they were the only species reported at three sites, including one island and two island-like structures (Table 1). Twelve co-nesting colonial waterbird species were documented at cormorant nesting locations (Fig. 5). Most sites (89%) were shared with herring

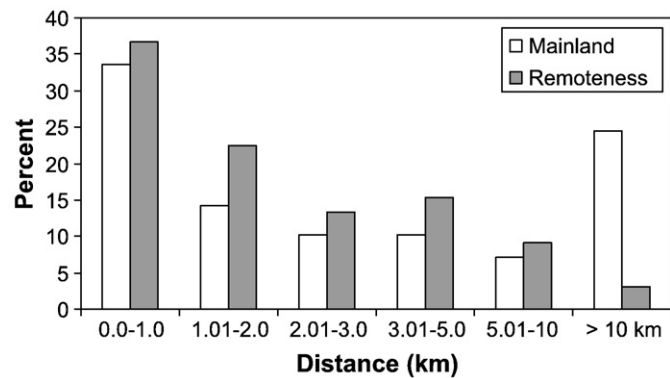


Fig. 3. Distance from mainland and remoteness of sites used by double-crested cormorants in U.S. Great Lakes. (Remoteness value based on shortest of two distances measured from breeding site to mainland and to nearest island inhabited by humans or mammalian predators).

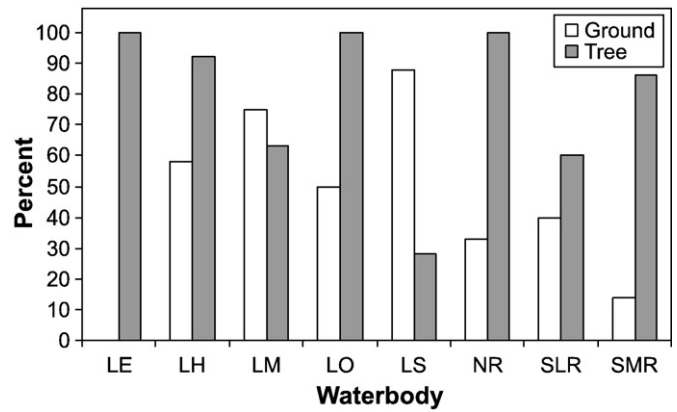


Fig. 4. Island sites used by double-crested cormorants characterized by ground and/or tree-nesting in each waterbody (LE = Lake Erie; LH = Lake Huron; LM = Lake Michigan; LO = Lake Ontario; LS = Lake Superior; NR = Niagara River; SLR = St. Lawrence River; SMR = St. Marys River).

gulls (*Larus argentatus*); other frequent nesting associates included ring-billed gulls (*Larus delawarensis*), black-crowned night-herons (*Nycticorax nycticorax*) and great blue herons (*Ardea herodias*), present at 41, 31 and 26% of sites occupied by cormorants, respectively (Fig. 5).

History of use by other nesting colonial waterbird species prior to occupation by cormorants was available for 77% of cormorant sites. Based on these data, a total of 10 colonial waterbird species was present at sites before and during colonization by cormorants (Fig. 5). Cormorants rarely (3%) colonized sites unoccupied by other colonial nesters. Sites with a history of use by herring gulls were most frequently colonized, comprising 95% of sites occupied by cormorants. Ring-billed gulls, great blue herons and black-crowned night-herons had a history of use and were present at 20–30% of sites colonized, while the remaining six colonial waterbird species were present at < 10% of sites colonized (Fig. 5).

*Colony sizes*

Colony size ranges were assigned to 58 of the 100 known colony sites (Table 1, Fig. 6); the 42 excluded sites had inadequate data to meaningfully characterize the site in terms of representative colony size for number of years occupied (Table 1). The majority of colonies (55%) were small to moderate (< 501 pairs), but a substantial portion (33%) were large (> 1000 pairs). Colony size was positively correlated (R = 0.67) with number of years occupied. All large colonies had been active for at least 12 years; on average, they existed for

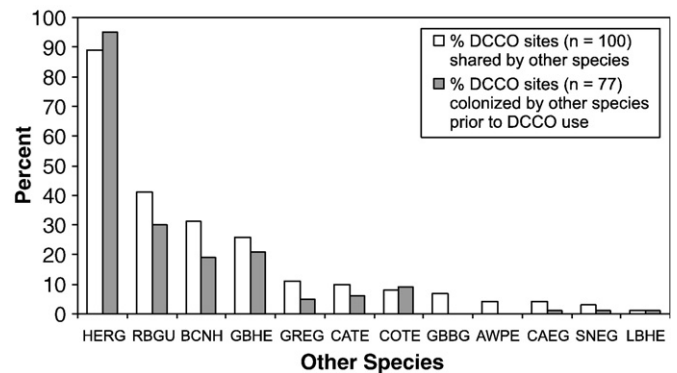


Fig. 5. Percent of double-crested cormorant (DCCO) sites shared by each co-nesting colonial waterbird species, and percent colonized by each co-nesting colonial waterbird species prior to occupancy by DCCOs.

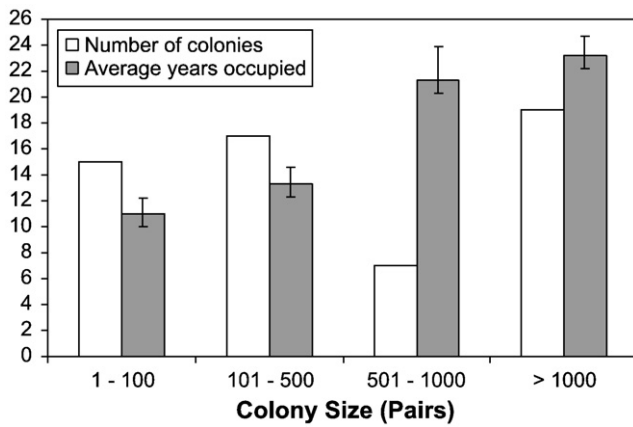


Fig. 6. Colony size ranges of double-crested cormorants on the U.S. Great Lakes and average (+/–SE) number of years occupied.

23 years +/– 1.5 years (SE). Most large colonies were in lakes Michigan (63%) and Huron (26%), and most (89%) were active in 2007 (Table 1). Colony size was not correlated with island area ( $R=0.13$ ), distance from mainland ( $R=0.02$ ) or island remoteness ( $R=0.22$ ). However, large colonies (>1000 pairs) developed almost exclusively (95%) on island sites >1.0 ha (Table 1), and almost twice as remote ( $n=19$ , mean = 3.6 km +/– 0.74 SE) as sites supporting small or mid-sized colonies ( $n=40$ , mean = 2.1 km +/– 0.38 SE). Additionally, the majority of large colonies were observed on islands where cormorants nested in trees and on the ground. Most (63%) small colonies ( $\leq 100$  pairs) were on islands <1.0 ha, and birds nested on the ground at 69% of these sites (Table 1).

## Discussion

### Characteristics of cormorant colonies

Sites are often identified for bird conservation or management based on the size of the populations they support; large aggregations frequently receive highest priority (e.g., Wires and Cuthbert, 2001; Ewert et al., 2004; Patrikeev, 2006; USDA, 2005, 2006a,b, 2008; Birdlife International, 2009). However, many factors determine whether a site will be used, number of years it will be occupied, and size a colony will attain. Therefore, understanding features of sites that attract birds to nest, and colonies to persist, can enhance conservation and management efforts.

Fundamental breeding site requirements for cormorants include appropriate space and substrate for nesting and safety from ground predators (Hatch and Weseloh, 1999; Trexel, 2002). Although proximity to high quality foraging areas is also an essential requirement (Hatch and Weseloh, 1999), analysis of this spatial component was beyond the scope of this work. The cormorant's basic need for sites safe from ground predators likely influences selection of islands in the narrow size range of 0.51–10 ha, and limits sites suitable for successful reproduction. Island biogeography theory predicts that increased area will result in greater habitat and species diversity (MacArthur and Wilson, 1967). Great Lakes islands on which mammalian predators persist must be large enough to support a consistent prey base. Home range sizes for coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and raccoon (*Procyon lotor*), common predators found on some Great Lakes islands, are highly variable but typically much larger than the island size range preferred by cormorants. Of the nine large (>10 ha) islands used during the 30 year study period, only six were active in 2007, and these appeared to have exceptional features (e.g., management actions to enhance habitat for colonial waterbirds, species compositions, island spatial characteristics) that likely made them suitable for cormorants despite their large size.

Safety from floods and extreme events also limits sites appropriate for nesting. Ludwig (1974) reported that small, low-lying islands in the Great Lakes are regularly flooded or submerged, resulting in abandonment by ring-billed gulls. Although we did not estimate elevation of islands used by nesting cormorants, our analysis did indicate that cormorants selected very small islands (<0.51 ha) less frequently than expected, and typically occupied them for shorter time periods than larger islands. For example, although 37% of colonies were on very small islands, on average they were active for only 6.8 years. In contrast, colonies on islands >0.5 ha were active on average 14.9 years. Additionally, most colonies (86%) on very small islands were used by <501 pairs, and many colonies on small islands (36%) were not active in 2007. An analysis of island elevation may help explain the island-size range selection patterns observed.

While there is likely an optimal island size range that enables a cormorant colony to persist and attain large size, it may vary to some extent with island remoteness. On average, the atypically large islands (>10 ha) used by cormorants were more remote than the characteristic islands (<10 ha) used. Close proximity to the mainland may influence island biodiversity (MacArthur and Wilson, 1967) and increase predation risk (Blokpoel and Scharf, 1999). Large remote islands may be suitable for cormorant nesting because predators may not reach them frequently enough to form stable populations. Additionally, many large islands in the Great Lakes have been developed by humans or have mammalian predators so proximity to these islands may also influence biodiversity and predation risk. The observation that large colony sizes (>1000 pairs) were on average found on more remote islands than smaller colonies ( $\leq 1000$  pairs) suggests island remoteness may also be an important predictor for large colony size. Furthermore, remoteness may also predict colony persistence, because colonies that existed for 16 or more years were on average more remote than colonies that persisted for <16 years (3.3 km vs. 2.3 km).

Ability to use tree or ground substrates for nesting provides a wider selection of islands for nesting cormorants than for other colonial nesters that utilize only trees or ground. On specific water bodies, however, cormorant colonies are characterized by tree- or ground-nesting, and substrate used appears to be a function of habitat availability rather than preference. For example, appropriate island habitat in Lake Erie exists mainly in the western basin, and appears limited. Of the 14 islands in the Bass Island Archipelago in U.S. waters, nine have some degree of residential development. The islands that appear suitable for cormorants are predominantly forested and all islands used in Lake Erie are occupied by tree-nesting birds. Conversely, most islands used in Lake Superior are occupied by ground-nesting cormorants because appropriate island habitat can be described as small islands composed of bedrock and simple plant communities, limited woody vegetation, and low human activity. Substrates used can also be influenced by length of time a site is occupied. Most large colonies (>1000 pairs), active on average 23 years, occur on islands where cormorants nest in trees and on the ground. Shifts to ground-nesting are often observed when trees die and fall after years of cormorant use (Weseloh and Ewins, 1994; Moore et al., 1995).

Presence of other nesting colonial waterbirds may also be an important predictor of sites likely to be used by cormorants. Although colonial waterbirds have been documented nesting on 771 sites in the U.S. Great Lakes since the Great Lakes Colonial Waterbird Survey was initiated, this is a small proportion (25%) of the total islands present. However, cormorants almost always colonize islands already occupied by other colonial nesting species, especially herring gulls. In Denmark, work describing sites colonized by great cormorants (*Phalacrocorax carbo*) identified the presence of breeding herons as one of three important site characteristics, and suggested their presence indicated information about a site's safety (Bregnballe and Gregersen, 1995). Similarly, in the Great Lakes the presence of herring

gulls and other colonial waterbirds may indicate absence of mammalian predators and proximity to abundant food resources, and thus convey important information to cormorants about a site's quality.

#### *Cormorants within the Great Lakes island landscape*

Although cormorants are not the most abundant colonial waterbird species in the U.S. Great Lakes (Cuthbert et al., 2010), their numbers are perceived as the most problematic by some citizens and policy makers. Concern over impacts has resulted in intensive management of this species and highly charged politics in this area (USFWS, 2003b). Rapid population growth within the region since the 1970s, coupled with specific behavior (e.g., fish consumption; destruction of vegetation) led to the emergence of negative public attitudes towards cormorants. In fishing communities, especially (e.g., Les Cheneaux Islands and Saginaw Bay, Lake Huron, MI; Eastern Basin, Lake Ontario, NY), anti-cormorant sentiments have developed as people associated the birds with local sport and commercial fish declines (Lounsbury, 2000; Fleisher, 2002; McGrath, 2003).

To reduce local resource conflicts largely in this area, a Public Resource Depredation Order (PRDO) (USFWS, 2003a) was established for cormorants in 2003. Under this order control of breeding colonies on Great Lakes waters began in 2004, mostly on Michigan and New York waters (USDA, 2004; McCullough et al., 2008); prior to this time it occurred at a limited number of sites in New York waters under depredation permits (Wires et al., 2001). It did not become a widespread practice on the U.S. Great Lakes (i.e., occur on all five Great Lakes) until 2006, when the states of OH and WI also began implementing cormorant management activities (USDA, 2006a, 2008). Additionally, in 2006, the state of Michigan amended its Environmental Assessment for cormorant control to significantly increase its control efforts (USDA, 2006b). By 2007, most cormorant colonies (64%) active in the U.S. Great Lakes had experienced some control measure authorized under the PRDO or other depredation permit. Conversely, on the Canadian Great Lakes comparatively little management occurs; non-experimental control activities have been undertaken at only three of the 160 cormorant colonies documented since the 1970s.

Most sites (90%) in U.S. waters considered in this analysis were colonized before control activities began under the PRDO; only 2–6% were colonized in 2007 when control was widespread. Therefore, the distribution and characteristics of cormorant colony sites described here largely reflect the preferences of birds relatively free from human pressure. However, if cormorant control continues as a long-term and widespread activity, the distribution and characteristics of cormorant colony sites in this region may eventually reflect options available to an intensively managed population. Additionally, because most (82%) sites with large numbers active in 2007 were experiencing legal control in an effort to reduce numbers, criteria for sites identified for conservation may shift from those with large numbers (>1000 pairs, Wires and Cuthbert, 2001) to sites that sustain small numbers.

The near shore waters of the Great Lakes are heavily used by humans in a variety of ways, and also provide critical habitat for waterbirds (Edsall, 1997). Double-crested cormorants typically forage in waters close to shore (<5 km, Hatch and Weseloh, 1999), and in the U.S. Great Lakes, they frequently choose nest sites in near shore waters (this study). Stapanian and Bur (2002) found that overlap in habitat use by humans and cormorants in western Lake Erie may lead to the perception that cormorants are a threat to fisheries. Similarly, certain characteristics of cormorant breeding sites and proximity to shoreline or large developed islands may influence how cormorants are perceived by humans. For example, changes in vegetation following cormorant use can occur rapidly (Bédard et al., 1995) and are more dramatic on small islands than on large ones. Because cormorants frequently nest on relatively small islands in trees, often

close to areas utilized by humans, the perception of severe and widespread impacts to Great Lakes islands from cormorants (Glahn et al., 2000; USFWS, 2003b) may be exacerbated.

However, when cormorant presence is considered at the scale of the island resource, presence is in fact small; cormorants occupy a very small number of islands and a fraction of island space within the U.S. Great Lakes island landscape. Additionally, if the scale of this analysis were expanded to include the Canadian Great Lakes islands, cormorant presence would appear even smaller. Based on the 260 known cormorant colony sites and >31,000 islands Great Lakes-wide (with 90% in Canada, Dan Kraus, personal communication), cormorants have occupied <1% of Great Lakes islands.

To gain understanding of their relative importance, impacts to island resources from cormorants should be considered in the broader context of island science, island conservation priorities and known island threats. Recently, projects have been completed for the Great Lakes to assess major threats to island biodiversity (Vigmostad et al., 2007) and to identify islands important for conservation based on biodiversity values (Henson et al., 2010). Incorporating geographic scope, severity and reversibility, the threat assessment identified habitat loss and fragmentation, overharvest, contaminants, invasive species, and climate change as the five major threats to Great Lakes island biodiversity. Based on the conservation assessment, very few U.S. islands of high conservation significance were occupied by cormorants. This may be due partly to the fact that cormorants typically nest on relatively small islands that are fairly near shore. Conversely, islands that earned high scores in the conservation assessment often did so because of their larger size and potential to support a greater range of species and communities. Additionally many were located at a greater distance from the mainland and were identified as important as stopover sites for migrant birds or as representatives of unique ecological systems relatively free of human impacts (Henson et al., 2010). Considering characteristics of islands used by cormorants, and proportion of islands and island area affected, threats to island biodiversity from cormorants may be comparatively local and small-scale in nature. In addition, cormorants are part of island biodiversity. While this awareness may not change human attitudes toward cormorants, understanding cormorant population size and colony site use within an island-landscape context is important for managers faced with decisions about cormorant control, and conversely, conservation.

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#### **References**

- Bédard, J., Nadeau, A., Lepage, M., 1995. Double-crested cormorant culling in the St. Lawrence River estuary. *Waterbirds* 18 (Special Publication 1), 78–85.
- BirdLife International, 2009. Important Bird Areas (IBAs). <http://www.birdlife.org/action/science/sites/2009>.

- Blokpoel, H., 1977. Gulls and terns nesting in northern Lake Ontario and the upper St. Lawrence River. Canadian Wildlife Service Progress Notes 75. 12 pp.
- Blokpoel, H., McKeating, G.B., 1978. Fish-eating birds nesting in Canadian Lake Erie and adjacent waters. Canadian Wildlife Service Progress Notes 87. 12 pp.
- Blokpoel, H., Ryder, J.P., Seddon, I., Carswell, W.R., 1980. Colonial waterbirds nesting in Canadian Lake Superior in 1978. Canadian Wildlife Service Progress Notes 118. 13 pp.
- Blokpoel, H., Scharf, W.C., 1999. The importance of the islands of the Great Lakes as nesting habitat for colonial waterbirds. In: Vigmostad, K.E. (Ed.), State of the Great Lakes Islands: Proceedings from the 1996 U.S.–Canada Great Lakes Islands Workshop. Department of Resource Development. Michigan State University, East Lansing, pp. 32–41.
- Bregnballe, T., Gregersen, J., 1995. Changes in growth of the breeding population of cormorants *Phalacrocorax carbo sinensis* in Denmark. Suppl Ric Biol Selvag XXVI, 31–46.
- Coleman, J.T.H., Richmond, M.E., 2007. Daily foraging patterns of adult double-crested cormorants during the breeding season. Waterbirds 30, 189–198.
- Crispin, Susan, 1999. The global significance of Great Lakes islands. In: Vigmostad, K.E. (Ed.), State of the Great Lakes Islands: Proceedings from the 1996 U.S.–Canada Great Lakes Islands Workshop. Department of Resource Development. Michigan State University, East Lansing, pp. 6–10.
- Cuthbert, F.J., Wires, L.R., McKearnan, J.E., 2002. Potential impacts of nesting double-crested cormorants on great blue herons and black-crowned night-herons in the U.S. Great Lakes region. J Great Lakes Res 28, 145–154.
- Cuthbert, F.J., McKearnan, J., Wires, L.R., Joshi, A., 2010. Distribution and abundance of colonial waterbirds in the US Great Lakes: 1997–1999. Final report to U.S. Fish and Wildlife Service, Ft. Snelling, MN.
- Edsall, T., 1997. Nearshore waters of the Great Lakes. State of the Lakes Ecosystem Conference 1996. Background paper. ISBN 0-662-26031 / EPA 905-R-97-015a / Cat. No. En40-11/35-1-1997E. [http://www.epa.gov/solec/solec\\_1996/Nearshore\\_Waters\\_of\\_the\\_Great\\_Lakes.pdf](http://www.epa.gov/solec/solec_1996/Nearshore_Waters_of_the_Great_Lakes.pdf).
- Ewert, D.N., DePhilip, M., Kraus, D., Harkness, M., Froehlich, A., 2004. Biological ranking criteria for the conservation of islands in the Laurentian Great Lakes. Final report to the U.S. Fish and Wildlife Service. [http://www.nature.org/wherework/northamerica/greatlakes/files/usfws\\_island\\_ranking\\_rpt\\_2004dec10\\_final.pdf](http://www.nature.org/wherework/northamerica/greatlakes/files/usfws_island_ranking_rpt_2004dec10_final.pdf).
- Flesher, J., 2002. Angry anglers rail against bird. Petoskey News-Review. Pp.A-1, A-10. January 10, 2002.
- Glahn, J.F., Tobin, M.E., Blackwell, B.F., 2000. A Science-Based Initiative to Manage Double-Crested Cormorant Damage to Southern Aquaculture. U.S. Department of Agriculture/APHIS/WS 11-55-010.
- Hatch, J.J., Weseloh, D.V., 1999. Double-crested cormorant (*Phalacrocorax auritus*). In: Poole, A., Gill, F. (Eds.), The Birds of North America, No. 441. The Birds of North America, Inc., Philadelphia, PA.
- Hebert, C.E., Weseloh, D.V., Senese, E.M., Haffner, G.D., 2005. Unique island habitats may be threatened by double-crested cormorants. J Wildl Manage 69 (1), 68–76.
- Henson, B.L., Kraus, D., McMurtry, M.J., Ewert, D.N., 2010. Islands of life: A biodiversity and conservation atlas of the Great Lakes islands. Nature Conservancy of Canada. 154 pp.
- Johnsgard, P.A., 1993. Cormorants, Darters and Pelicans of the World. Smithsonian. Inst. Press, Washington, D.C.
- Lounsbury, H., 2000. No Sanctuary, vol. 127(191). The Bay Times Press, pp. 1A–4A. July 9, 2000.
- Ludwig, J.P., 1974. Recent changes in the ring-billed gull population and biology in the Laurentian Great Lakes. Auk 91, 575–594.
- MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.
- McCullough, R.D., Farquhar, J.F., Mazzocchi, I.M., 2008. Cormorant Management Activities in Lake Ontario's Eastern Basin. New York State Department of Environmental Conservation. Lake Ontario Annual Report 2008. Section 13:1–7. [http://www.dec.ny.gov/docs/fish\\_marine\\_pdf/lorpt08sec13.pdf](http://www.dec.ny.gov/docs/fish_marine_pdf/lorpt08sec13.pdf).
- Mcgrath, S., 2003. Shootout at Little Galloo. Smithsonian Magazine. February 2003.
- Mercer, D.M., 2008. Phylogeography and population genetic structure of double-crested cormorants (*Phalacrocorax auritus*). M.S. Thesis, Oregon State University.
- Moore, D.J., Blokpoel, H., Lampman, K.P., Weseloh, D.V., 1995. Status, ecology and management of colonial waterbirds nesting in Hamilton Harbour, Lake Ontario, 1988–1994. Technical Report Series No. 213. Canadian Wildlife Service, Ontario Region.
- Neuman, J., Pearl, D.L., Ewins, P.J., Black, R., Weseloh, D.V., Pike, M., et al., 1997. Spatial and temporal variation in the diet of double-crested cormorants (*Phalacrocorax auritus*) breeding on the lower Great Lakes in the early 1990s. Can J Fish Aquat Sci 54, 1569–1584.
- Palmer, R.S., 1962. Handbook of North American Birds, Vol. 1. Yale University Press, New Haven and London.
- Patrikeev, M., 2006. Conservation priorities for colonial waterbirds in the Canadian sector of the Great Lakes. Draft report prepared for the Canadian Wildlife Service. Environment Canada, Ontario, Canada. 30 pp.
- Scharf, W.C., 1978. Colonial birds nesting on man-made and natural sites in the U.S. Great Lakes. Technical report D-78-10. U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi.
- Scharf, W.C., Shugart, G.W., 1998. In: Bowerman, W.W., Roe, A.S. (Eds.), Distribution and abundance of gull, tern and cormorant nesting colonies of the U.S. Great Lakes, 1989 and 1990. Publication, vol. 1. Gale Gleason Environmental Institute, Lake Superior State University Press, Sault Ste. Marie, MI.
- Seefelt, N.E., 2005. Foraging ecology, bioenergetics and predatory impact of breeding double-crested cormorants (*Phalacrocorax auritus*) in the Beaver Archipelago, Northern Lake Michigan. Doctoral Dissertation, Michigan State University, East Lansing, Michigan.
- Stapanian, M.A., Bur, M.T., 2002. Overlap in offshore habitat use by double-crested cormorants and boaters in western Lake Erie. J Great Lakes Res 28, 172–181.
- The Nature Conservancy, 2006. Spatial database of U.S. Great Lakes islands. The Nature Conservancy, Central U.S. Conservation Region. GIS Lab, Minneapolis, MN.
- Trexel, D.R., 2002. Double-crested cormorant (*Phalacrocorax auritus*) breeding population trends and colony site selection in northern lakes Michigan and Huron during recovery from extirpation (1970–2001). M.S. Thesis, University of Minnesota, St. Paul, MN.
- USACE and GLC, 1999. Living with the Lakes. Understanding and Adapting to Great Lakes Water Level Changes. U.S. Army Corps of Engineers and Great Lakes Commission 0-9676123-0-6. <http://www.glc.org/living/pdf/lakelevels.pdf>.
- USDA (U.S. Department of Agriculture), 2004. Environmental Assessment: Reducing Double-crested Cormorant damage in Michigan. USDA, APHIS, WS, Okemos, Michigan. [http://www.aphis.usda.gov/regulations/ws/ws\\_nepa\\_environmental\\_documents.shtml](http://www.aphis.usda.gov/regulations/ws/ws_nepa_environmental_documents.shtml).
- USDA, 2005. Environmental Assessment: Reducing Double-Crested Cormorant Damage in Minnesota. USDA, APHIS, WS, St. Paul, MN. [http://www.aphis.usda.gov/regulations/ws/ws\\_nepa\\_environmental\\_documents.shtml](http://www.aphis.usda.gov/regulations/ws/ws_nepa_environmental_documents.shtml).
- USDA, 2006a. Environmental Assessment: Reducing Double-Crested Cormorant Damage in Ohio. USDA, APHIS, WS, Reynoldsberg, OH. [http://www.aphis.usda.gov/regulations/ws/ws\\_nepa\\_environmental\\_documents.shtml](http://www.aphis.usda.gov/regulations/ws/ws_nepa_environmental_documents.shtml).
- USDA, 2006b. Final Amendment to the Environmental Assessment Reducing Double-Crested Cormorant Damage through an Integrated Wildlife Damage Management Program in the State Of Michigan. USDA, APHIS, WS. <http://www.fws.gov/Midwest/nepa/MICormorantNEPA/documents/AmendmenttoDCCOFinal2006.pdf>.
- USDA, 2008. Environmental Assessment: Reducing Double-Crested Cormorant Damage in Wisconsin. USDA, APHIS, WS, Sun Prairie, WI. [http://www.aphis.usda.gov/regulations/ws/ws\\_nepa\\_environmental\\_documents.shtml](http://www.aphis.usda.gov/regulations/ws/ws_nepa_environmental_documents.shtml).
- USFWS (U.S. Fish and Wildlife Service), 2003a. Migratory bird permits; regulations for double-crested cormorant management, Final rule. Fed Regist 68 (195), 58022–58037 [October 8, 2003].
- USFWS, 2003b. Final Environmental Impact Statement: Double-Crested Cormorant Management. U.S. Department of Interior Fish and Wildlife Service in cooperation with U.S. Department of Agriculture APHIS Wildlife Services. <http://www.fws.gov/migratorybirds/CurrentBirdIssues/Management/cormorant/CormorantFEIS.pdf>.
- Vigmostad, K.E. (editor), 1999. State of the Great Lakes Islands: Proceedings from the 1996 U.S.–Canada Great Lakes Islands Workshop. Department of Resource Development, Michigan State University, East Lansing, MI.
- Vigmostad, K., Cuthbert, F.J., Ewert, D.N., Greenwood, R., Kraus, D., Seymour, M., et al., 2007. Great Lakes islands: biodiversity elements and threats. A final report to the Great Lakes National Program Office of the Environmental Protection Agency. [http://www.nemw.org/GLIslands\\_final\\_report\\_07.pdf](http://www.nemw.org/GLIslands_final_report_07.pdf) Last accessed July 21, 2008.
- Weseloh, D.V., Mineau, P., Teeple, S.M., Blokpoel, H., Ratcliff, B., 1986. Colonial waterbirds nesting in Canadian Lake Huron in 1980. Canadian Wildlife Service Progress Notes 165. 28 pp.
- Weseloh, D.V., Ewins, P.J., 1994. Characteristics of a rapidly increasing colony of double-crested cormorants (*Phalacrocorax auritus*) in Lake Ontario: population size, reproductive parameters and band recoveries. J Great Lakes Res 20, 443–456.
- Weseloh, D.V., Ewins, P.J., Struger, J., Mineau, P., Bishop, C.A., Postupalsky, S., et al., 1995. Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproductive output between 1913 and 1991. Colonial Waterbirds 18 (Special Publication 1), 48–59.
- Weseloh, D.V., Pekarik, C., Havelka, T., Barrett, G., Reid, J., 2002. Population trends and colony locations of double-crested cormorants in the Canadian Great Lakes and immediately adjacent areas, 1990–2000: a manager's guide. J Great Lakes Res 28 (2), 125–144.
- Wires, L.R., Cuthbert, F.J., 2001. Identification and prioritization of colonial waterbird nest sites for conservation in the U.S. Great Lakes. Final Report to U.S. Fish and Wildlife Service. Fort Snelling, MN.
- Wires, L.R., Cuthbert, F.J., Trexel, D.R., Joshi, A.R., 2001. Status of the double-crested cormorant (*Phalacrocorax auritus*) in North America. Final Report to U.S. Fish and Wildlife Service. Fort Snelling, MN.
- Wires, L.R., Cuthbert, F.J., 2006. Historic populations of the double-crested cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st Century. Waterbirds 29, 9–37.
- Wires, L.R., Lewis, S.J., Soulliere, G.J., Matteson, S.M., Weseloh, D.V., Russell, R.P., et al., 2010. Upper Mississippi Valley/Great Lakes Waterbird Conservation Plan. Final report to U.S. Fish and Wildlife Service, Fort Snelling, MN.