WETLANDS, Vol. 26, No. 2, June 2006, pp. 605–611

NOTE

ASSESSING THE SENSITIVITY OF WETLAND BIRD COMMUNITIES TO HYDROLOGIC CHANGE IN THE EASTERN GREAT LAKES REGION

David A. Steen[1,3], James P. Gibbs[1], and Steven T. A. Timmermans[2]
[1]*State University of New York College of Environmental Science and Forestry*
350 Illick Hall, 1 Forestry Drive
Syracuse, New York, USA 13210

[2]*Bird Studies Canada*
P.O. Box 160
Port Rowan, Ontario, Canada, N0E 1M0

[3]*Present address:*
Joseph W. Jones Ecological Research Center
Route 2, Box 2324
Newton, Georgia, USA 39870
E-mail: David.Steen@jonesctr.org

Abstract: Uncertainty about the effects of ongoing natural and anthropogenic changes to Great Lakes ecosystems, such as managed stabilized water levels, coupled with widespread public interest regarding status of wetland birds prompted us to evaluate sensitivity of regional wetland birds to hydrologic changes. We reviewed published literature to determine preferred habitat of 30 wetland birds in the region, emphasizing vegetation required for foraging and nesting during the breeding season. Species were subsequently assigned to one of three risk categories based on association with vegetation types sensitive to water-level stabilization, as well as nesting height above water. Notably, of the bird species designated as low, moderate, and high risk, 25%, 33%, and 63%, respectively, have been regionally declining based on Bird Studies Canada's Marsh Monitoring Program. This evaluation may be useful to regional biologists, planners, and managers concerned with predicting how particular species might be affected by future hydrologic changes in this and related systems.

Key Words: bird populations, Great Lakes, habitat loss, hydrology, Lake Ontario, waterbirds, water level management

INTRODUCTION

Relatively little is known regarding the biology of wetland-associated birds. These birds include some of the most unique species (e.g., grebes and bitterns) and some of the most abundant species (e.g., Red-winged Blackbird; see Table 1 for scientific names), as well as many charismatic and endangered species (e.g., Black Tern). Numbers of many wetland bird species are decreasing in North America (Eddleman et al. 1988, Conway and Eddleman 1994), including in the Great Lakes region (Timmermans et al. 2004). The primary factor for these declines is likely habitat loss and degradation, including wetland habitat alteration caused by anthropogenic manipulation of hydrologic cycles.

Diversity of wetland bird communities is widely considered to be associated with the diversity of wetland flora, as well as spatial complexity of their juxtaposition with one another on the landscape (Gibbs et al. 1991). Consequently, any ecological processes that tend to simplify or homogenize wetland habitats will likely do so to the detriment of wetland-associated bird communities. Stabilizing water levels or managing them outside the range of historic fluctuations eliminates the dynamic patterns that allow a diversity of wetland species and communities to thrive (Bedford 1990). Such is the case in the Great Lakes region, where one consequence of decades of water-level management on Lake Ontario has been a tendency for fringing wetlands to become more densely vegetated and dominated by cattail (*Typha* spp.) and invasive species such as purple loosestrife, (*Lythrum salicaria*

Table 1. Habitat preferences and nest heights of Lake Ontario wetland birds. Citations upon which this synthesis is based are available from the authors.

Species	Nest Height (m)	Foraging Habitats[2]	Nesting Habitats	Population Trend[3]
High Risk[1]				
Pied-billed Grebe *Podilymbus podiceps* Linnaeus	<1	OW; SV; EV	OW; SV; EV	Decrease
American Coot *Fulica americana* Gmelin	<1	OW; SV	OW; EV	N/A
Common Moorhen *Gallinula chloropus* Linnaeus	<1	SV; EV	EV; SV	Decrease
Black Tern *Chlidonias niger* Linnaeus	<1	OW; EV	OW, EV	Decrease
Caspian Tern *Sternia caspia* Pallas	<1	OW	SDG	Increase
Virginia Rail *Rallus limicola* Vieillot	<1	OW; EV	EV	Increase
Marsh Wren *Cistothorus palustris* Wilson	<1	EV	EV	Decrease
Least Bittern *Ixobrychus exilis* Gmelin	<1	EV	EV	Decrease
Sora *Porzana carolina* Linnaeus	<1	EV; SS; MF	EV; SS	Increase
Moderate Risk				
Belted Kingfisher *Ceryle alcyon* Linnaeus	Variable	OW	B	Decrease
Red-winged Blackbird *Agelaius phoeniceus* Linnaeus	Variable	EV	EV; SS; MF; OT	Increase
Northern Shoveler *Anas clypeata* Linnaeus	<1	OW; SV	MF	N/A
Swamp Sparrow *Melospiza georgiana* Latham	<1	OW; EV; SS; S	EV; SS; S	Increase
Blue-winged Teal *Anas discors* Linnaeus	<1	SV; EV; SS	EV; SS; MF	Increase
Gadwall *Anas strepera* Linnaeus	Variable	SV	SS; S	Increase
Green-winged Teal *Anas crecca* Linnaeus	<1	SV; EV	SS; MF	N/A
American Bittern *Botaurus lentiginosus* Rackett	<1	EV; SS; S	EV; MF; SS	Decrease
Common Snipe *Gallinago gallinago* Linnaeus	<1	SS; EV	OW; SS; S	N/A
Low Risk				
Great Blue Heron *Ardea herodias* Linnaeus	>1	OW; MF, SV, EV	OT	Increase
Black-crowned Night Heron *Nycticorax nycticorax* Linnaeus	>1	OW; SV; EV	EV; SS; S; OT	Decrease

Table 1. Continued.

Species	Nest Height (m)	Foraging Habitats[2]	Nesting Habitats	Population Trend[3]
American Wigeon *Anas americana* Gmelin	<1	SV; EV; MF	S; MF	N/A
Canada Goose *Branta canadensis* Linnaeus	<1	SV; MF	EV; MF	Increase
Mallard *Anas platyrhynchos* Linnaeus	<1	EV; MF	EV; SS; MF	Increase
Green Heron *Butorides striatus* Linnaeus	>1	EV	S; OT	Increase
Sedge Wren *Cistothorus palustris* Wilson	<1	SS; S; MF	SS; S; MF	N/A
Alder Flycatcher *Empidonax alnorum* Brewster	<1	S; MF; OT	S; OT	Increase
American Black Duck *Anas rubripes* Brewster	Variable	SV; EV; SS	EV; S; OT	N/A
Willow Flycatcher *Empidonax traillii* Audubon	>1	EV, S	S; OT	Increase
Common Grackle *Quiscalus quiscula* Linnaeus	>1	MF	OT	Decrease
Northern Harrier *Circus cyaneus* Linnaeus	<1	MF	MF	N/A

[1] Risk levels corresponded to a species' potential response to stabilized water levels based on microhabitats and vegetation used for nesting and foraging during their breeding season.
[2] Habitat Codes: OW: Open Water; SV: Submergent Vegetation; EV: Emergent Vegetation; SDG: Sand/Dirt/Gravel; B: Banks; MF: Meadow/Field; OT: Open Timber; SS: Scrub/Sedge; S: Shrub.
[3] Population trends were based on data collected in Lake Ontario coastal marshes.

L.) and/or common reed, (*Phragmites australis* (Cav.) Trin. ex Steud., (Wilcox 1990, Wilcox 1993, Wilcox et al. 1993, Hudon 1997, Beland 2003, Farrell et al. 2004), a tendency that runs counter to the maintenance of ''hemi-marsh'' situations that benefit most wetland birds species (Gibbs et al. 1991). Water-level management in Lake Ontario, initiated with operation of the St. Lawrence Seaways, has reduced water-level fluctuations from about 2 m to approximately 0.9 m since 1976 (Wilcox 1993) and has eliminated year-to-year variation (Wilcox and Whillans 1999).

Artificially minimizing water-level fluctuations may negatively affect wetland bird populations adapted to aquatic microhabitats. This would likely be achieved through direct loss of microhabitats most closely associated with wetlands, such as submergent vegetation. Birds that rely on these microhabitats for foraging and nesting would likely be at greater risk to water level management. To assess how water-level stabilization might influence the wetland bird community in the Great Lakes region, we reviewed the published literature to identify local- and landscape-scale linkages between wetland characteristics and wetland bird diversity. We related this information to ongoing population trends of wetland birds in the region to determine if the species that should be most susceptible to water-level regulation are the species actually declining. Such information is important to synthesize so that ramifications of various water level regulation scenarios, as mediated by changes in wetland vegetation, can be evaluated for the significant wetland bird communities that occupy the region.

SELECTION OF SPECIES AND METHODS OF LITERATURE REVIEW

We chose species for our study that were native, wetland obligates and those relatively common in Lake Ontario wetlands (percent occurrence on Bird Studies Canada's Marsh Monitoring Program counts from 1995 to 2002 at 107 points on Lake Ontario marshes of $> 1\%$), or those that were rare (occurrence $< 1\%$), but nevertheless of conservation concern because of dependence on wetland habitat, importance as game species, or have experienced population declines (Timmermans et al. 2004). Of all species detected in Lake Ontario marshes during this period, 30 met these criteria (Table 1). We assembled literature by searching computerized databases using Cambridge Scientific Abstracts—Biological Science, BiblioLine's Wildlife Worldwide and The Birds of North America—Life Histories for the 21st Century series.

CLASSIFICATION OF SPECIES INTO RISK CATEGORIES

Based on the literature survey of individual species habitat associations (summarized in Table 1), we divided the 30 bird species into three categories: low, moderate, and high risk. These risk levels corresponded to a species' potential response to stabilized water levels based on microhabitats and vegetation used for nesting and foraging during their breeding season. A species was classified as being at ‘‘low risk’’ if it tended to nest in vegetation over one meter in height in wetlands or in upland habitat at any height, such as meadow or open timber. Low risk species also foraged either exclusively in habitat unlikely to be directly affected by water-level stabilization or in several types of habitat. For example, the Great Blue Heron qualified as a low risk species according to our criteria because it nests in timber 30 m or more above ground and feeds in a wide variety of habitats.

Bird species were classified as being at ‘‘moderate risk’’ if they foraged in habitat sensitive to water-level stabilization but either nest exclusively in vegetation over one meter in height in wetlands or in upland habitat. For example, Northern Shovelers are considered moderate risk because they forage primarily in open water but are also known to associate closely with submergent vegetation; such microhabitats are likely to be influenced by water level and displacement of submergent vegetation by persistent emergents such as cattail. Although a ground nester, the Northern Shoveler prefers vegetation associated with meadow and field habitats, such as grass and nettles.

A ‘‘high risk’’ species nested < 1m above the water exclusively in wetland habitats. These species foraged on vegetation that could be adversely affected by human-controlled water levels. An example of a high risk species is the Pied-billed Grebe, which nests on floating vegetation among and occasionally anchored to emergent vegetation and is highly dependent on floating-leaved and submergent vegetation for foraging. The Pied-billed Grebe's nesting and foraging habits are sufficient to categorize it as high risk.

CONTRASTING PREDICTED SENSITIVITY WITH POPULATION TREND

We used data collected by Bird Studies Canada's Marsh Monitoring Program volunteer participants, who surveyed bird abundance and occurrence throughout coastal marsh habitats of Lake Ontario between 1995 and 2002. Prior to their first survey season (May–July), participants were given training kits that included survey protocol instructions, data forms, instructional cassette tapes with examples of songs and calls of common wetland birds, and a call-broadcast tape that was used during surveys to elicit vocal responses from Virginia Rail, Sora, American Bittern, Least Bittern, Common Moorhen, American Coot, and Pied-billed Grebe (Weeber and Vallianatos 2000).

After reviewing survey protocol and completing a self-training exercise, participants established survey routes in wetlands $\geq$1 ha in size. Depending on wetland size, survey routes consisted of from one to eight (maximum) different survey stations. Survey stations were defined as 100-m-radius semicircles that contained $\geq$50% coverage of emergent vegetation where birds were counted each year. The center of each survey station was the focal point from which observers recorded bird counts; these were permanently marked with a stake and metal tag to ensure relocation in subsequent visits within and among years. Each station was $\geq$ 250 m from another, which minimized duplicate counts of individual birds within routes. Most routes were established at the ecotone between wetland and drier upland habitats, but some participants also surveyed routes in wetland interiors.

Bird surveys were conducted twice annually at each station between 20 May and 5 July, and survey visits were temporally spaced by at least 10 days. Surveys were conducted after 1800 hours EST on days when there was no precipitation, the temperature exceeded 16 ° C, and wind speed was less than 20 $\mathrm{km{\cdot}hr^{-1}}$ (3 on the Beaufort scale). Birds were counted for 10 minutes during each survey station visit in the following manner. At each focal point, volunteers played a 5-minute call broadcast tape (each species call listed above separated by 30 seconds of silence) and recorded all birds heard and/or seen within each survey station during the call playback period and a 5-minute silent listening period immediately following the playback period. Birds flying up to a height of 100 m over survey stations were also recorded.

Bird abundance indices for Lake Ontario coastal wetlands were calculated in the following manner. First, species count data for stations within routes were summarized to provide one value for each species detected on each route. We used Generalized Linear Models with a Poisson error distribution (PROC GEN-

MOD; SAS Institute Inc. 1990) to generate annual abundance indices for each species. These ‘‘route-regression’’ models were designated as Species Count (Y) = Year (class), Route (class). We ran 1,000 iterations of each model to stabilize variances and to derive mean annual abundance estimates for each species. These values were scaled to correct for possible overdispersion before transforming into abundance indices for trend analyses (PROC GENMOD, PSCALE option; SAS Institute Inc. 1990). Annual estimated species counts (i.e., class coefficients) were converted into abundance indices using the following formula:

$$\text{Abundance Index} = e^{\text{A}\times\text{M}} \qquad (1)$$

where

e = 2.7183 which is the base of the natural logarithm
A = annual estimated species count (i.e., class coefficients) from route-regression models
M = mean number of individuals counted on all routes in the final survey year.

This transformation allowed us to determine relative (percent) annual differences in bird abundance indices scaled to the average value for the most recent survey year.

Species-specific relative abundance trends for birds counted in Lake Ontario coastal wetlands during the 1995–2002 study period were calculated and evaluated for biological significance and statistical reliability using Generalized Linear Models (PROC GENMOD; SAS Institute Inc. 1990). The same input data, error distribution, and regression modeling structures and procedures as described above for calculating abundance indices were used for these analyses, except that ‘‘Year’’ was included as a continuous variable to provide a linear estimated rate of change (i.e., trend) in each species’ abundance through time. Species-specific slope estimates (corrected for overdispersion) from route-regression models were converted into relative indices of change (abundance trends) by using the following formula:

$$\text{Abundance trend} = 100 \times (e^{\exists} - 1) \qquad (2)$$

where

e = 2.7183 which is the base of the natural logarithm
$\exists$ = Year coefficient from species-specific route-regression models.

This transformation allowed us to determine percent annual change in bird abundance indices during 1995–2002. Likelihood ratio tests were used to calculate the probability that year effects (slopes) differed from zero. To do this, differences in model deviance between those with and without year effects were calculated; those differences (based on 1 error degree of freedom) were used to obtain probabilities from a chi-squared distribution, which were subsequently converted (1—chi-square probability) into P-values (Collett 1994).

To determine whether our risk classifications corresponded with the status of species in the Lake Ontario basin, we contrasted the assigned risk with current species population trends at coastal wetlands of Lake Ontario, which were available for 22 of the 30 birds included in the risk designation analysis (T. 2). Birds for which trend data were not available included American Wigeon, Green-winged Teal, American Black Duck, Sedge Wren, Common Snipe, Northern Shoveler, Northern Harrier, and American Coot. Data were considered reliable for a species if it was observed at over 10 sites. Seven species were only recorded at five to nine sites (Table 2).

Of the bird species designated as low, moderate, and high risk in this study, we found 25%, 33%, and 63%, respectively, to be decreasing according to the Marsh Monitoring Program (not including birds for which there were no trend data available). While not statistically significant, likely due to small sample size, these results suggest a strong relationship between vulnerability to hydrologic changes as estimated from our reviews of these species’ natural history and ongoing changes in their populations in the region.

SYNTHESIS

Although many factors influence population status of these species in the region, including coastal development, environmental contamination, erosion, and predation (Wires and Cuthbert 2001), the corroboration we observed between assigned risk and wetland birds abundance suggest indirectly that regional hydrologic change could be an important driver of contemporary population trends in these species. Bird populations dependent on microhabitats that are likely most affected by stabilizing water levels are those evidently declining in the Great Lakes region. These declines may be due to the management history of Lake Ontario, which has resulted in wetland degradation due to water-level change divergent from that resulting from natural processes (Wilcox 1990, Wilcox 1993, Hudon 1997). While there are disadvantages associated with fluctuating water levels, such as increased risk of nest loss and susceptibility to predation, recent, anthropogenic alterations of the water cycle likely influence wetland-associated bird populations on a larger scale than these natural sources of mortality, as populations have not had the necessary time to adapt to these changes. Further research may be required to de-

Table 2. Population trends of wetland bird species in Lake Ontario coastal wetlands for which trend data were available, as recorded by the Marsh Monitoring Program (1995–2002).

Species	% Change/Year	P	Upper CI	Lower CI
Alder Flycatcher[1]	20.31	0.19	61.02	−10.10
American Bittern[1]	−13.51	0.19	26.08	−40.67
Black-crowned Night Heron	−7.60	0.38	9.58	−22.09
Belted Kingfisher	−12.23	0.19	4.82	−26.50
Black Tern	−32.15	<0.001	−14.50	−46.15
Blue-winged Teal[1]	9.46	0.41	45.45	−17.63
Canada Goose	3.17	0.72	21.80	−12.61
Caspian Tern[1]	7.58	0.57	40.30	−17.51
Common Grackle	−1.41	0.82	18.36	−17.87
Common Moorhen	−5.76	0.24	3.79	−14.44
Gadwall[1]	10.31	0.43	38.74	−12.29
Great Blue Heron	7.99	0.18	21.37	−3.91
Green Heron	8.52	0.34	29.24	−8.88
Least Bittern[1]	−2.80	0.77	20.09	−21.34
Mallard	3.59	0.50	15.28	−6.92
Marsh Wren	−0.46	0.88	6.01	−6.54
Pied-billed Grebe[1]	−33.29	<0.001	−4.73	−53.28
Red-winged Blackbird	1.01	0.61	5.05	−2.88
Sora	4.60	0.57	22.75	−10.86
Swamp Sparrow	5.03	0.07	10.71	−0.36
Virginia Rail	2.10	0.61	10.72	−5.85
Willow Flycatcher	2.74	0.61	13.31	−6.84

[1] These species were observed at 5–9 sites, all others were observed at a minimum of 10 sites. Accordingly, trend data for these species are less reliable.

termine why birds we designated as low risk are still declining.

It is important also to note that, in addition to the specific habitat components emphasized in this study, wetland area and isolation has a profound influence on wetland bird community structure and diversity. With regard to bird communities, increasing habitat area has been found to increase wetland bird species richness in Iowa (Brown and Dinsmore 1986), Maine (Gibbs et al. 1991), North Carolina (Mamo and Bolen 1999), and Ontario (Findlay and Houlahan 1997). In Great Lakes coastal wet meadows, habitat area was the best single predictor of bird abundance and species occurrence (Riffel et al. 2001), and a complex wetland landscape increased species richness, abundance, and probability of patch-use (Riffel et al. 2003). Although the percentage of wetlands within a complex covered by emergent vegetation was the single most important variable when explaining variation in species richness in Iowa, the amount of wetland habitat surrounding a particular area was also a significant predictor (Fairbairn and Dinsmore 2001). In addition, the presence of several wetland bird species in South Dakota was positively related to the amount of available habitat (Naugle et al. 1999). Wetland area and diversity of habitats afforded by large wetland areas are essential parameters to consider when attempting to effectively conserve wetland bird communities. It is likely that management scenarios reducing the amount of suitable wetland bird habitat will result in a decrease in species richness. These decreases may be apparent and ongoing in the Lake Ontario and perhaps Lake Superior basins due to their water-management history and resulting habitat alteration.

ACKNOWLEDGMENTS

Funding for this work was provided to the State University of New York's College of Environmental Science and Forestry by the International Joint Commission's Lake Ontario—St. Lawrence River Study Board via the U.S. Army Corps of Engineers. Manuscript preparation was made possible by support to the Joseph W. Jones Ecological Research Center at Ichauway. K. L. Coffey and several anonymous reviewers provided comments on the manuscript. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc. in the USA and other countries.

LITERATURE CITED

Bedford, B. 1990. Increasing the scale of analysis: the challenge of cumulative impact assessment for Great Lakes wetlands. Proceedings: International Symposium on Wetlands of the Great Lakes, Niagara Falls, NY, USA.
Beland, M. 2003. Holocene vegetation dynamics of an upper St.

Lawrence River coastal wetland and surrounding uplands: Effects of climate change and anthropogenic disturbance. M.S. Thesis. State University of New York College of Environmental Science and Forestry, Syracuse, NY, USA.

Brown, M. and J. J. Dinsmore. 1986. Implications of marsh size and isolation for wetland birds management. Journal of Wildlife Management 50:392–397.

Collett, D. 1994. Modelling Binary Data. Chapman and Hall, London, UK.

Conway, C. J. and W. R. Eddleman. 1994. Virginia rail. p. 193–206. In T. C. Tacha and C. E. Braun (eds.) Migratory Shore and Upland Game Bird Management in North America. International Association of Fish and Wildlife Agencies, Washington, DC, USA.

Eddleman, W. R., F. L. Knopf, B. Meanley, F. A. Reid, and R. Zembal. 1988. Conservation of North American rallids. Wilson Bulletin 100:458–475.

Fairbairn, S. E. and J. J. Dinsmore. 2001. Local and landscape-level influences on wetland birdcommunities on the prairie pothole region of Iowa, USA. Wetlands 21:41–47.

Farrell, J., J. Toner, A. Halpern, M. Beland, B. Murry, A. Cushing, K. Hawley, and D. Leopold. 2004. Restoration of coastal wetlands in the St. Lawrence River through the re-establishment of natural hydrologic regimes. Final report to the Great Lakes Protection Fund, Chicago, IL, USA.

Findlay, C. S. and J. Houlahan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation Biology 11:1000–1009.

Gibbs, J. P, J. R. Longcore, D. G. McAuley, and J. K. Ringelman. 1991. Use of wetland habitats by selected nongame water birds in Maine. United States Fish and Wildlife Service, Resource Publication 9, Washington, DC.

Hudon, C. 1997. Impact of water-level fluctuations on St. Lawrence River aquatic vegetation. Canadian Journal of Aquatic Science 54: 2853–2865.

Mamo, L. B. and E. G. Bolen. 1999. Effects of area, isolation, and landscape on the avifauna of Carolina Bays. Journal of Field Ornithology 70:310–320.

Naugle, D. E., K. F. Higgins, S. M. Nusser, and W. C. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology 14:267–276.

Riffell, S. K., B. E. Keas, and T. M. Burton. 2001. Area and habitat relationships of birds in Great Lakes coastal wet meadows. Wetlands 21:492–507.

Riffell, S. K., B. E. Keas, and T. M. Burton. 2003. Birds in North American Great Lakes coastal wet meadows: is landscape context important. Landscape Ecology 18:95–111.

SAS Institute Inc. 1990. SAS/STAT User's Guide Version 6, fourth edition. SAS Institute Inc., Cary, NC, USA.

Timmermans, S. T. A., S. S. Badzinski, and K. E. Jones. 2004. The Marsh Monitoring Program annual report, 1995–2002: Annual indices and trends in bird abundance and amphibian occurrence in the Great Lakes basin. Bird Studies Canada, Port Rowan, ON, Canada.

Weeber, R. C. and M. Vallianatos. 2000. The Marsh Monitoring Program 1995–1999: monitoring Great Lakes wetlands and their amphibian and bird inhabitants. Bird Studies Canada, Port Rowan, ON, Canada.

Wilcox, D. A. 1990. Water-level fluctuations and Great Lakes wetlands. Great Lakes Wetlands 1:1–3.

Wilcox, D. A. 1993. Effects of water-level regulation on wetlands of the Great Lakes. Great Lakes Wetlands 4:1–2, 11

Wilcox, D. A., J. H. Meeker, and J. Elias. 1993. Impacts of water-level regulation on wetlands of the Great Lakes. Phase 2 Report to Working Committee 2, International Joint Commission Water-Levels Reference Study, Ottawa, Ontario, Canada and Washington, DC, USA.

Wilcox, D. A. and T. H. Whillans. 1999. Techniques for restoration of disturbed coastal wetlands of the Great Lakes. Wetlands 19: 835–857.

Wires, L. R. and F. J. Cuthbert. 2001. Prioritization of waterbird colony sites for conservation in the U.S. Great Lakes. Final Report to United States Fish and Wildlife Service. Fort Snelling, MN, USA.

Manuscript received 14 April 2005; revisions received 12 September 2005 and 17 November 2005; accepted 6 February 2006.