STABLE ISOTOPE INVESTIGATIONS OF FORAGING ECOLOGY: IMPLICATIONS FOR

COLONIAL WATERBIRD CONSERVATION AND MANAGEMENT

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

Elizabeth Carol Craig

May 2015

STABLE ISOTOPE INVESTIGATIONS OF FORAGING ECOLOGY: IMPLICATIONS FOR
COLONIAL WATERBIRD CONSERVATION AND MANAGEMENT

Elizabeth Carol Craig, Ph. D.

Cornell University 2015

Human interactions with colonial waterbirds occur on a continuum, from wildlife conservation at
one end, to human-wildlife conflict at the other. This dissertation explored cases across this
continuum, using stable isotopes to elucidate foraging behaviors critical to waterbird
conservation and management issues. The first research chapter (Chapter 2) examined the type of
foraging habitats used by colonial waterbirds in New York Harbor. For six species, key foraging
habitat types were identified in order to prioritize the protection of foraging sites based on the
resources they provided. Chapter 3 employed a captive feeding approach to measuring diet-tissue
discrimination (measurements critical for SI diet analysis) in the Double-crested Cormorant. The
remainder of this dissertation focused on the consumption of farmed fish by Double-crested
Cormorants (*Phalacrocorax auritus*) in the southeastern US. These chapters provided novel
approaches for remotely and noninvasively identifying birds involved in depredation (Chapter 4),
and, as opposed to observing the effects of cormorants on aquaculture as was traditional in this
field, considered the reciprocal effect of aquaculture on the birds (Chapter 5). The findings of
Chapter 4 provided dietary (i.e., isotopic) confirmation of previously observed patterns of
migratory connectivity. Breeding colonies in the Great Lakes contained the greatest proportion
of birds that had consumed aquaculture resources during the winter. However, some proportion
of every breeding population sampled across the eastern United States wintered in aquaculture

habitats. We concluded that management of breeding birds in the Great Lakes was unlikely to alleviate aquaculture depredation, as birds breeding further west and east might increasingly contribute to the problem. Chapter 5 evaluated the importance of seasonal interactions in the life history of cormorants, specifically the strength of the carry-over effect of winter foraging behavior on summer body condition and reproductive output. Counter to our expectations, there was little support for a carry-over effect on body condition or reproductive output. In summary, this dissertation demonstrated the value of applying SI to a range of wildlife conservation and management issues, and supported the use of SI as a non-invasive, and relatively cost-effective method of monitoring resource use in wildlife populations.

BIOGRAPHICAL SKETCH

Elizabeth's interests in birds and in the marine world reach back to her early childhood. Hands on experiences attending John's Hopkins summer camps in marine biology and working at wild bird rehabilitation centers at The Chewonki Foundation in Maine (2002 -2003) and The Raptor Trust in New Jersey (2003-2008) solidified Elizabeth's passion for birds and wildlife conservation. While studying as an undergraduate at Columbia University in the department of Ecology, Evolution and Environmental Biology (2003-2007), Elizabeth realized that she could turn her passion into a vocation, and began to explore wildlife conservation as a potential career. With the guidance of Dr. Susan Elbin, along with Columbia University faculty, Elizabeth achieved departmental honors for her research of colonial waterbirds in New York Harbor, and her undergraduate work earned a best student paper award from the International Association of Great Lakes Research. After graduating from Columbia University (*summa cum laude* and Phi beta kappa), Elizabeth continued her work with Susan, first as a Program Assistant at Wildlife Trust (2007) and then as a Research Associate at the New York City Audubon Society (2008-present), where she conducted research and monitoring of colonial waterbirds in New York Harbor. In 2008, Elizabeth began her graduate studies in the field of Zoology and Wildlife Conservation at Cornell University's College of Veterinary Medicine. Based on her interests in colonial waterbirds, Elizabeth undertook a laboratory rotation with Dr. Milo Richmond, learning about his Common Tern (*Sterna hirundo*) conservation work on Oneida Lake; a program that, after Milo's retirement, she succeeded him in managing. Elizabeth then undertook a lab rotation with Dr. Paul Curtis, who subsequently became the chair of her graduate committee based on their common interest in human-wildlife interactions, particularly concerning the Double-crested Cormorant (*Phalacrocorax auritus*). For her dissertation research, Elizabeth collaborated with

biologists from the United States Department of Agriculture, Animal and Plant Health Inspection Service-Wildlife Services to apply stable isotope techniques to explore the interactions between cormorants and the aquaculture industry in the southeastern United States. During her time at Cornell, Elizabeth also served as a teaching assistant for five courses, and was acknowledged as an Outstanding Graduate Teaching Assistant in the Department of Natural Resources. She also co-lectured Applied Population Ecology with Dr. Evan Cooch, and guest lectured for audiences at Cornell and beyond. Elizabeth has given dozens of scientific talks, and her graduate research was recognized by the Waterbird Society, an international society of waterbird biologist, earning a best student paper award. In 2014, Elizabeth was elected as a member of the Waterbird Society's Executive Council.

ACKNOWLEDGMENTS

Before thanking the people that contributed to this dissertation, I want to take this opportunity to acknowledge the birds involved in my research. While I am proud to have taken advantage of existing management programs to the greatest extent possible as a source of bird tissue, I am still keenly aware of the sacrifice of life. I am, therefore, all the more grateful for the opportunities that I have had to conduct my research remotely and noninvasively. It is a great

privilege to work with this incredible group of birds, and I hope that my research will serve to advance colonial waterbird conservation efforts.

I am grateful for the professional and personal support and guidance of my graduate committee, chaired by Paul Curtis, and including Susan Elbin, Jed Sparks, Lars Rudstam and Ned Place. Paul's guidance has been invaluable in navigating graduate school. I also greatly value our shared fieldwork experiences working with waterbirds on Oneida Lake, and look forward to continuing to work together on this project in the future. Jed Sparks, in addition to helping me build a solid foundation in stable isotope ecology, deserves special thanks for including me in the regular activities of his lab group. Feedback from the Sparks lab has been invaluable in the editing of my dissertation chapters, and has greatly improved nearly every major presentation I have written. From the Sparks lab, I would like to extend my warm regards to Fiona Soper, Rasa Zalakeviciute, and Kirsten Deane-Coe for being great colleagues and friends over the course of my graduate career. Lars and Ned, who took less of an active role in my specific research projects, provided invaluable perspective for my work as a whole, and I thank them both for always being available and generous with their time. Finally, of all the members on my committee, Susan has worked with me the longest, and she has played a profound role in my professional and personal development. I am truly thankful that, in addition to being my mentor, teacher, sometimes boss, and friend, Susan was willing and able to serve as an ad-hoc member on my committee. I am thankful to all of my committee members for being positive and supportive through every phase of my research.

I owe the success of my graduate research to the many collaborators, technicians, and administrators that worked with me along the way. First I would like to thank my collaborators at NWRC: Brian Dorr, Katie Hanson-Dorr, Tommy King, and their supervisor, Fred Cunningham.

times when they were most needed.

I'd like to acknowledge mentors and colleagues that have not directly collaborated on my research, but have greatly influenced my science and my professional development. Chip Weseloh has been a mentor to me in the world of cormorant biology since we met during my undergraduate years studying waterbirds in New York Harbor. Chip taught me to band cormorants, and carry four cormorant chicks at a time. He (and Susan) also taught me the value of great networking and interpersonal skills, and the importance of getting out in the field with collaborators. I believe it is Chip's influence that has made the field of cormorant biology in this part of the world so collaborative. I hold the sentiment that every end of a cormorant is the "business end" of a cormorant, and I thank Chip and Susan both for teaching me to work confidently and safely with these impressive animals. I would also like to thank Dave Moore for encouraging me as a young, aspiring waterbird biologist, and the many staff members of the USDA and New York State Department of Environmental Conservation who have been great colleagues and collaborators on all my colonial waterbird management and conservation work. Finally I'd like to acknowledge Keith Hobson and Craig Hebert for their role in inspiring much of my research concerning the application of stable isotope techniques to colonial waterbirds ecology. Craig Hebert's presentation on the application of sulfur stable isotopes to cormorant foraging behavior (at the International Association of Great Lakes Research conference in 2007) was the first time I ever got excited about stable isotopes. Craig has continued to be a valued colleague and I look forward to working with him more in the future. Keith Hobson's foundational work in applying stable isotopes to waterbird ecology is inspirational in and of itself. I am incredibly grateful to consider Keith a colleague, and have greatly valued his advice over the years.

Another major aspect of my graduate career has been teaching. I have served as a teaching assistant for a number of courses over a wide range of topics in my years as a graduate student. By far my most formative teaching experiences were in Evan Cooch's course in Applied Population Ecology. I had the great fortune to assist Evan for three years, and by the third time around, Evan entrusted his students to me for a number of core lectures. Evan taught me to turn off powerpoint and pick up the chalk. He is an excellent lecturer and I hope to have gleaned a few lessons from him in that respect. He is also an excellent mentor, and under his supervision I gained what confidence and skill I have in front of a classroom.

I want to conclude my acknowledgements by extending my heartfelt thanks to my family and friends. My loving parents, John and Judy Craig, have always supported and indulged me in exploring my passions. By doing this, they have encouraged me to pursue a fulfilling path in life, and provided me with the perspective to appreciate what is truly important, both professionally and personally. They have a distinct gift for showing their support by incorporating my passions into their own lives, from exploring wild bird photography to joining the board of the New York City Audubon Society. I want to thank the rest of my family and friends for supporting me throughout the graduate school experience, and conclude by thanking my dog, Sunny, for her company while writing my dissertation, and my partner in crime, Tyler Hale, for making the last few years of my life a joy, and for helping me always keep my eye on the big picture.

TABLE OF CONTENTS

LIST OF FIGURES

xi

LIST OF TABLES

CHAPTER 1

INTRODUCTION

Colonial waterbirds – definitions, conservation, and management

In this dissertation, I use stable isotope techniques to explore foraging behavior of colonial waterbirds in order to inform conservation and management action. Colonial waterbirds are aquatic birds that nest communally, typically on islands or other isolated habitats. This is a diverse, cosmopolitan, and polyphyletic group of birds, including gulls and terns, long-legged wading birds, and diving birds such as pelicans and cormorants. Colonial waterbirds are intrinsically linked to both terrestrial and aquatic environments, relying on limited terrestrial nesting habitats to raise young, and aquatic habitats, ranging from fresh- and saltwater marsh to open water, for foraging. Many of these species also occupy top trophic positions, and are therefore sensitive to conditions throughout the food webs in which they forage. From an applied perspective, interactions between humans and colonial waterbirds occur on a continuum, from conservation of threatened and endangered species at one end, to human-wildlife conflict at the other. My dissertation explores cases across this continuum, using stable isotopes to elucidate foraging behavior that is critical to waterbird conservation and management issues.

Stable isotope analysis – definitions and applications to foraging ecology

The use of stable isotope analysis has become widespread in studies of wildlife diet and foraging ecology, as the isotopic value observed in the tissue of an animal reflects that of its diet (DeNiro and Epstein 1978, Inger and Bearhop 2008). Stable isotope values are discussed throughout this dissertation using delta notation: $\delta X = (R_{sample} - R_{standard})/R_{standard}) \times 1000$, where X is, for example, ^{13}C, ^{15}N or ^{34}S, and R is the corresponding ratio of heavy to light isotopes (e.g.,

1

^{13}C/^{12}C, ^{15}N/^{14}N or ^{34}S/^{32}S) in either the sample of interest (R$_{sample}$) or an international reference standard (R$_{standard}$). Stable isotope values serve as records of the biogeochemical processes of a system, and with careful interpretation, isotopic values of elements such as carbon (δ^{13}C), nitrogen (δ^{15}N), and sulfur (δ^{34}S) can be used to monitor diet, relative trophic position, and foraging habitat of birds (Bond and Jones 2009).

δ^{13}C values primarily indicate the source of carbon at the base of the food web in which an animal has foraged. More negative (lower) δ^{13}C values can indicate a greater proportion of freshwater resource use, while less negative (higher) δ^{13}C values can indicate a greater proportion of marine resource use (Mizutani et al. 1990, Hobson and Clark 1992a, Bearhop et al. 1999, Bond and Jones 2009). Inclusion of C$_4$ photosynthetic plant materials in the diet, such as products containing corn or cane sugar, can also create higher δ^{13}C values (Farquhar et al. 1989). Such values may indicate use of anthropogenic resources such as human food waste or intensive aquaculture (Hebert et al. 2009).

δ^{15}N values primarily indicate the relative trophic position at which a bird has foraged, as δ^{15}N increase with every trophic exchange (Steele and Daniel 1978, Minagawa and Wada 1984, Hobson and Clark 1992a, Bond and Jones 2009). Values of δ^{15}N are also influenced by the nutritional status of the bird (Sears et al. 2008) as well as the isotopic value at the base of the food web. Caution was taken, therefore, when interpreting δ^{15}N in terms of trophic position without prior knowledge of δ^{15}N signatures at the base of the food web (Post 2002).

The final stable isotope used in this research, δ^{34}S, is highly influenced by whether sulfur fixation occurred in freshwater or marine environments (Lott et al. 2003) and is therefore useful in identifying the extent of marine versus freshwater resources use.

For the majority of this research, I conducted stable isotope analysis on feathers. These

tissues, like human hair and fingernails, are isotopically inert once formed (Hobson and Clark 1992b), and therefore contain information on diet and foraging behavior at the time they were grown. This is significant, as we can learn about past foraging behavior by analyzing feathers grown at different periods of time. Feathers can also be collected non-invasively, creating opportunities to address a broader range of questions and study systems.

Dissertation structure

This dissertation is organized as a series of four independent papers for journal publication, and therefore there are some redundancies within the text of each chapter. These chapters addressed issues spanning the continuum of human-waterbird interactions, with Chapter 2 focusing on conservation, and the remaining chapters addressing issues of human-wildlife conflict.

Chapter 2: Conserving important foraging habitat for colonial waterbirds in New York Harbor

My first research chapter, entitled "Conserving important foraging habitat for colonial waterbirds in an urban estuary: a stable isotope approach," examined the type of foraging habitats that colonial waterbirds breeding in New York Harbor used to provision their young. The Harbor Heron Conservation Plan of the New York/New Jersey Harbor Estuary Program recently called for research to expand our understanding of colonial waterbird foraging behavior in this system (Harbor Herons Subcommittee 2010). To this end, I investigated the use of foraging habitat through stable isotope analysis of nestling waterbird feathers. This study included species that spanned the range in phylogeny, conservation status, and foraging strategy

within the waterbird community of New York Harbor. Half of the species in this study were of greatest conservation need according to New York State Department of Environmental Conservation (New York State Department of Environmental Conservation 2014), including the Great Egret (*Ardea alba*), Black-crowned Night-Heron (*Nycticorax nycticorax*), and Glossy Ibis (*Plegadis falcinellus*). The second half included more common species: the Herring Gull (*Larus argentatus*), Great Black-backed Gull (*Larus marinus*), and Double-crested Cormorant (*Phalacrocorax auritus*). For each species I determined the key foraging habitat types used by adults to provision their young in order to prioritize the protection of foraging habitats based on the relative importance of the resources they provide. This chapter gave me the opportunity to apply stable isotope techniques to a familiar system (Craig 2009, Craig et al. 2012, Craig 2013), and to contribute to the conservation management of colonial waterbirds in New York Harbor.

Chapters 3-5: Double-crested Cormorants – foraging behavior, management, and life history implications

The following three chapters of my dissertation focused on a single species, the Double-crested Cormorant, a piscivorous colonial waterbird native to North America. On the continuum of human-waterbird interactions, this species finds itself at the human-wildlife conflict extreme, and is therefore of interest from a wildlife management as well as an ecological perspective. Since the 1970s, the Double-crested Cormorant has undergone rapid population expansion throughout much of its historic range (Hatch 1995, Hatch and Weseloh 1999, Weseloh et al. 2002, Ridgway et al. 2006, Wires and Cuthbert 2006). Population increases have been ascribed to lower mortality due to decreased contaminant levels, reduced human persecution, and increased food sources including aquaculture (Glahn et al. 1997, Hatch and Weseloh 1999,

4

Glahn and King 2004). Resulting cormorant abundance may place increasing pressure on foraging and nesting habitats. Cormorants can reduce habitat quality and destroy vegetation when nesting at high densities (Hebert et al. 2005, Kolb et al. 2012, Craig et al. 2012) and may compete for nesting habitat with co-occurring colonial waterbird species when nesting in mixed-species colonies (Cuthbert et al. 2002, Weseloh et al. 2002, Somers et al. 2007, 2011). Cormorants have also been implicated in a range of human conflict issues including competition with commercial and sport fisheries (Taylor and Dorr 2003, Rudstam et al. 2004, Diana et al. 2006, Dorr et al. 2012*b*), and impacts to aquaculture facilities (Glahn et al. 2002, Glahn and King 2004, Dorr et al. 2012*a*). Cormorants wintering at catfish farms in the southeastern U.S. impose an annual burden of as much as $25 million through predation on fish and associated management costs (Glahn et al. 2002). Pressure from the aquaculture industry, as well as from commercial and sport fishermen, has led to increased control efforts for cormorant populations at both wintering and breeding grounds (Glahn and Stickley 1995, Glahn et al. 2000*a*, 2000*b*, 2002, Tobin et al. 2002, Diana et al. 2006).

I undertook Chapter 3, entitled "Isotopic discrimination in the Double-crested Cormorant (*Phalacrocorax auritus*)" as a first fundamental step in applying stable isotope techniques to foraging studies in cormorants. As explained above, stable isotope analysis is useful in studies of wildlife diet and foraging ecology because the isotopic value observed in the tissue of an animal reflects that of its diet. However, as a consumer assimilates dietary nutrients into its own tissues, the isotopic values of those tissues may deviate from that observed in the original diet. This deviation is known as the isotopic discrimination factor. The extent of isotopic discrimination varies among species (Caut et al. 2009) such that, without the isotopic discrimination factor for the species in question, inferences about diet are subject to potential

error (Bond and Diamond 2011). To this end, I collaborated with USDA scientists in a captive feeding study they were undertaking, in order to measure discrimination factors in Double-crested Cormorant tissues for stable isotope ratios of carbon, nitrogen and sulfur. This provided an essential link for the use of stable isotopes in researching foraging ecology, diet, and resource use of this widespread and controversial species.

As aquaculture depredation is one of the major areas of conflict concerning cormorants, the remainder of my dissertation focused on developing stable isotope techniques to remotely identify cormorants consuming aquaculture resources, to track the distribution of birds using these resources, and to observe the potential effects of aquaculture resource use on cormorant populations. Chapter 4, entitled "Using stable isotopes to decipher winter habitat use of Double-crested Cormorants (*Phalacrocorax auritus*) breeding in eastern North America," describes the use of stable isotopes in feathers to remotely identify the type of foraging environments (aquaculture, natural freshwater, or marine) that cormorants used during the winter. By sampling winter-grown feathers from birds on the breeding grounds, I was able to determine what proportion of a breeding colony consumed aquaculture resources during the previous winter. I applied this approach to breeding colonies across the eastern portion of the species' breeding range in North America in order to observe spatial patterns in winter resource use, and identify areas of the breeding range that contributed significantly to aquaculture depredation during the winter.

The final research chapter of my dissertation, Chapter 5, entitled "Seasonal interactions play a limited role in Double-crested Cormorant (*Phalacrocorax auritus*) life history," explored the potential influences of aquaculture resource use on cormorant populations. Researchers have hypothesized that, in addition to providing supplemental resources during the winter and

improving winter survival, use of aquaculture resources may provide cormorants with further advantage by improving condition and reproductive success during the subsequent breeding season (Glahn et al. 1997, Hebert et al. 2008). This phenomenon, in which events in one season create a carry-over effect into the following season, is called a seasonal interaction, and I set out to evaluate the importance of seasonal interactions in cormorant populations. This topic was of interest from a fundamental ecological perspective as well as a population management perspective. I addressed a question concerning the basic biology of cormorants (i.e., do seasonal interactions play an important role in the life history of this species?), while also considering the management implications (i.e., how has human land-use change, in this case increasing aquaculture in the southeastern United States, influenced cormorant populations?).

Chapter 6: Conclusion

In Chapter 6, the conclusion of this dissertation, I summarize the major findings of each research chapter and discuss the broader implications of my work in the context of wildlife conservation and management. My key findings ranged from novel observations of habitat use in species of conservation need in New York Harbor, to the surprisingly limited benefit that aquaculture may provide for cormorants wintering in the southeastern United States.

Summary

As a whole, this dissertation spans a range of topics, systems, and approaches. However, this work is unified by the application of stable isotope techniques to questions of foraging ecology of colonial waterbirds. My use of stable isotope techniques allowed me to overcome the

spatial and temporal constraints traditionally limiting questions of foraging ecology, and

provided a novel perspective to both the basic and applied ecology of this fascinating group of

birds.

REFERENCES

Bearhop, S., D. Thompson, S. Waldron, I. Russell, G. Alexander, and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants Phalacrocorax carbo shot at inland fisheries in England. Journal of Applied Ecology 36:75–84.

Bond, A. L., and A. W. Diamond. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecological Applications 21:1017–1023.

Bond, A., and I. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. Marine Ornithology 37:183–188.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

Craig, E. C. 2009. New York City Audubon's Harbor Herons Project: 2009 interim nesting survey. New York City Audubon, New York, NY.

Craig, E. C. 2013. New York City Audubon's Harbor Herons Project: 2013 nesting survey –28th annual report. New York City Audubon, New York, NY.

Craig, E. C., S. B. Elbin, J. A. Danoff-Burg, and M. I. Palmer. 2012. Impacts of Double-crested Cormorants (Phalacrocorax auritus) and other colonial waterbirds on plant and arthropod communities on islands in an urban estuary. Waterbirds 35 (special publication 1):4–12.

Cuthbert, F. J., L. R. Wires, and J. McKearnan. 2002. Potential impacts of nesting Double-crested Cormorants on Great Blue Herons and Black-crowned Night-Herons in the US Great Lakes region. Journal of Great Lakes Research 28:145–154.

DeNiro, M., and S. Epstein. 1978. Influence of diet on distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506.

Diana, J. S., S. L. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. Journal of Great Lakes Research 32:306–320.

Dorr, B. S., L. W. Burger, S. C. Barras, and K. C. Godwin. 2012*a*. Economic impact of Double-crested Cormorant, Phalacrocorax auritus, depredation on channel catfish, Ictalurus punctatus, aquaculture in Mississippi, USA. Journal of the World Aquaculture Society 43:502–513.

Dorr, B. S., S. L. Hanisch, P. H. Butchko, and D. G. Fielder. 2012*b*. Management of Double-crested Cormorants to improve sport fisheries in Michigan: three case studies. Human-Wildlife Interactions 6:155–168.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40:503–537.

Glahn, J. F., and D. T. King. 2004. Bird depredation. Pages 1–27 *in* C. Tucker and J. Hargreaves, editors. Biology and culture of channel catfish. Elsiver, Amersterdam, The Netherlands.

Glahn, J. F., M. E. Tobin, and B. F. Blackwell. 2000*a*. A science-based initiative to manage Double-crested Cormorant damage to southern aquaculture. USDA National Wildlife Research Center - Staff Publications. Paper 532.

Glahn, J. F., M. E. Tobin, and J. B. Harrel. 1997. Possible effects of catfish exploitation on overwinter body condition of Double-crested Cormorants. Symposium on Double-crested Cormorants: population status and management issues in the Midwest Paper 11:107–113.

Glahn, J., and A. R. Stickley Jr. 1995. Wintering Double-crested Cormorants in the Delta region of Mississippi: population levels and their impact on the catfish industry. Colonial Waterbirds 18:137–142.

Glahn, J., D. Reinhold, and C. Sloan. 2000*b*. Recent population trends of Double-crested Cormorants wintering in the Delta region of Mississippi: responses to roost dispersal and removal under a recent depredation order. Waterbirds 23:38–44.

Glahn, J., S. J. Werner, T. Hanson, and C. Engle. 2002. Cormorant depredation losses and their prevention at catfish farms: economic considerations. Pages 138-146 *in* L. Clark, editor. Human conflicts with wildlife: economic considerations. Proceedings of the third NWRC special symposium, Fort Collins, CO.

Harbor Herons Subcommittee. 2010. The Harbor Herons Conservation Plan- New York/New Jersey Harbor Region. S. B. Elbin and N. K. Tsipoura, editors. NY-NJ Harbor Estuary Program, New York, NY, USA.

Hatch, J. J. 1995. Changing populations of Double-crested Cormorants. Colonial Waterbirds 18:8–24.

Hatch, J. J. and D. V. C. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). No. 441 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hebert, C. E., D. V. C. Weseloh, A. Idrissi, M. T. Arts, and E. Roseman. 2009. Diets of aquatic birds reflect changes in the Lake Huron ecosystem. Aquatic Ecosystem Health & Management 12:37–44.

Hebert, C. E., J. Duffe, D. V. C. Weseloh, E. Senese, and G. Haffner. 2005. Unique island habitats may be threatened by Double-crested Cormorants. Journal of Wildlife Management 69:68–76.

Hebert, C. E., M. Bur, D. Sherman, and J. L. Shutt. 2008. Sulfur isotopes link overwinter habitat use and breeding condition in Double-crested Cormorants. Ecological Applications 18:561–567.

Hobson, K. A., and R. G. Clark. 1992*a*. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189–197.

Hobson, K. A., and R. G. Clark. 1992*b*. Assessing avian diets using stable isotopes I: turnover of 13C in tissues. Condor 94:181–188.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

Kolb, G. S., L. Jerling, C. Essenberg, C. Palmborg, and P. A. Hambäck. 2012. The impact of nesting cormorants on plant and arthropod diversity. Ecography 35:726–740.

Lott, C. A., T. Meehan, and J. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. Oecologia 134:505–510.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Mizutani, H., M. Fukuda, Y. Kabaya, and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk 107:400–403.

New York State Department of Environmental Conservation. 2014. New York species of greatest conservation need. <http://www.dec.ny.gov/docs/wildlife_pdf/sgcnlist.pdf>. Downloaded January 2015.

Post, D. 2002. The long and short of food-chain length. Trends in Ecology & Evolution 17:269–277.

Ridgway, M. S., J. B. Pollard, and D. V. C. Weseloh. 2006. Density-dependent growth of Double-crested Cormorant colonies on Lake Huron. Canadian Journal Of Zoology-Revue Canadienne De Zoologie 84:1409–1420.

Rudstam, L., A. VanDeValk, C. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14:149–163.

Sears, J., S. A. Hatch, and D. M. O'Brien. 2008. Disentangling effects of growth and nutritional status on seabird stable isotope ratios. Oecologia 159:41–48.

Somers, C. M., J. L. Doucette, D. V. C. Weseloh, V. A. Kjoss, and R. M. Brigham. 2011. Interactions between Double-crested Cormorants and other ground-nesting species. Waterbirds 34:168–176.

Somers, C. M., M. N. Lozer, and J. S. Quinn. 2007. Interactions between Double-crested Cormorants and Herring Gulls at a shared breeding site. Waterbirds 30:241–250.

Steele, K. W., and R. M. Daniel. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of 15N for tracer studies. Journal of Agricultural Science 90:7–9.

Taylor, J., and B. S. Dorr. 2003. Double-crested Cormorant impacts to commercial and natural resources. Wildlife Damage Management Conference 10:43–51.

Tobin, M. E., D. T. King, B. S. Dorr, S. J. Werner, and D. S. Reinhold. 2002. Effect of roost harassment on cormorant movements and roosting in the delta region of Mississippi. Waterbirds 25:44–51.

Weseloh, D. V. C., C. Pekarik, T. Havelka, G. Barrett, and J. Reid. 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. Journal of Great Lakes Research 28:125–144.

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the Double-crested Cormorant (Phalacrocorax auritus): implications for conservation and management in the 21st century. Waterbirds 29:9–37.

CHAPTER 2

CONSERVING IMPORTANT FORAGING HABITAT FOR COLONIAL WATERBIRDS IN
AN URBAN ESTUARY: A STABLE ISOTOPE APPROACH

Elizabeth Craig[1], Susan Elbin[2], Jed Sparks[3] and Paul Curtis[4]

[1] Field of Zoology and Wildlife Conservation,
Cornell University, Ithaca, NY, 14853, USA

[2] The New York City Audubon Society,
71 W. 23rd St., Suite 1523 New York, NY, 10010, USA

[3] Department of Ecology and Evolutionary Biology,
Cornell University, Ithaca, NY, 14853, USA

[4] Department of Natural Resources,
Cornell University, Ithaca, NY, 14853, USA

Abstract

Foraging habitat use of colonial waterbirds nesting in the New York/New Jersey Harbor estuary was examined to identify habitat types that were particularly important in terms of the relative proportion of resources they provided for adult diet and the subsequent provisioning of young. Stable isotope values of carbon, nitrogen, and sulfur were measured in nestling feathers from six waterbird species to determine the habitat type (ranging from marine to freshwater or anthropogenic) in which adults primarily foraged. These species included Black-crowned Night-Heron (*Nycticorax nycticorax*), Great Egret (*Ardea alba*), Glossy Ibis (*Plegadis falcinellus*), Double-crested Cormorant (*Phalacrocorax auritus*), Great Black-backed Gull (*Larus marinus*), and Herring Gull (*L. argentatus*). Waterbird populations exhibited both inter- and intra-specific variation in stable isotope values ($p < 0.001$) indicating variation in foraging habitat use among focal species across the estuary. Therefore, depending on the species- and region-specific conservation goal, management strategies would potentially need to target very different foraging habitats for protection and remediation. For instance, habitat use by Double-crested Cormorants closely reflected available habitat near nesting colonies, while Glossy Ibises utilized primarily freshwater resources at one colony and marine resources at another, despite the fact that both colonies were located in marine environments. Great Egrets and Double-crested Cormorants both showed significant regional variation in isotopic niche size, and both species of gulls, that were considered to be generalist scavengers, were found to have isotopic niche sizes reflecting a specialist diet. We suggest an integrative approach of observational methods and stable isotope analysis to facilitate the identification and prioritization of foraging sites for waterbird conservation.

Introduction

Colonial waterbirds have traditionally been considered as a single group with regards to conservation and management (Parnell et al. 1988, Kushlan 2012). This strategy has been effective for the protection of nesting habitat, as waterbirds often nest in mixed-species colonies, but its application to other breeding season habitats, such as foraging habitat, may be less effective. Mixed-species colonies can include birds with vastly different foraging behaviors and diets, reliant on a variety of foraging habitat types and resources. Further, a single species nesting on multiple islands within an estuary may use a range of different foraging habitats depending on the distance and quality of suitable resources. Foraging habitats chosen for waterbird conservation should be prioritized as a function of not only whether the habitat is being frequented, but also the relative energetic importance of the resource to the species of conservation concern. Conserving foraging habitat for waterbirds therefore presents a more complicated challenge than targeting breeding habitat alone.

The New York/New Jersey Harbor Estuary (the harbor), with an area of approximately 40,000 km^2, is home to approximately 20 million people. However, it also provides a mosaic of urban habitat types for wildlife, including open water, fresh- and saltwater marsh, uplands, and the built environment. Small, abandoned islands in the harbor have become important breeding areas for many of New York State's waterbirds since their resurgence in the region in the 1970s (Harbor Herons Subcommittee 2010). Sixteen waterbird species have been known to reproduce on these islands and forage in the surrounding wetlands and waterways to feed themselves and provision their young. Current knowledge and conservation efforts for these birds have generally focused on breeding population sizes and nesting phenology. The Harbor Heron Conservation Plan of the New York/New Jersey Harbor Estuary Program has recently called for research to

expand our understanding to include the foraging behavior of waterbirds in this system (Harbor

Herons Subcommittee 2010). To this end we investigated foraging resource use through stable

isotope analysis (SIA) of nestling waterbird feathers.

Stable isotope values are discussed here using delta notation:

$$\delta X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000 \qquad \text{(Equation 1)}$$

where X is ^{15}N, ^{13}C or ^{34}S, and R is the corresponding ratio of heavy to light isotopes (^{15}N/^{14}N,

^{13}C/^{12}C, or ^{34}S/^{32}S) in either the sample of interest (R_{sample}) or an international reference standard

($R_{standard}$). Reference standards for ^{15}N, ^{13}C and ^{34}S are atmospheric air, Vienna Pee Dee

Belemnite, and Vienna Canyon Diablo Troilite, respectively. Feather stable isotope values reflect

a bird's diet over the timescale of feather growth, and contain information about the relative

importance of foraging resources during that period (Hobson and Clark 1992*a*, *b*, Hobson 1999,

Inger and Bearhop 2008, Bond and Jones 2009). Feathers from nestling birds in particular

integrate the resources with which adult birds are provisioning their young, and are therefore

most suitable for answering questions about local foraging behavior and diet on the breeding

grounds (Cherel et al. 2000). Stable isotope values of a population can be considered to describe

an isotopic niche, analogous to the *n*-dimensional hypervolume of the ecological niche

(Hutchinson 1957), and defined as an area in δ-space (‰^{2}) with isotopic values as coordinates

(Newsome et al. 2007).

With careful interpretation, isotopic values of carbon (δ^{13}C), nitrogen (δ^{15}N), and sulfur

(δ^{34}S) can be used to monitor diet, relative trophic position, and foraging habitat of birds (Bond

and Jones 2009). δ^{13}C values in feathers primarily indicate carbon source at the base of the food

web in which the bird has recently foraged. More negative (lower) $\delta^{13}C$ values can indicate a greater proportion of freshwater resource use, while less negative (higher) $\delta^{13}C$ values can indicate a greater proportion of marine resource use (Mizutani et al. 1990, Hobson and Clark 1992b, Bearhop et al. 1999, Bond and Jones 2009). Inclusion of C_4 photosynthetic plant materials in the diet, such as products containing corn or cane sugar, can also create higher $\delta^{13}C$ values (Farquhar et al. 1989). Such values may indicate use of anthropogenic resources such as human food waste or intensive aquaculture (Hebert et al. 2009). $\delta^{15}N$ values primarily indicate the relative trophic position at which a bird has foraged, as $\delta^{15}N$ increase with every trophic exchange (Steele and Daniel 1978, Minagawa and Wada 1984, Hobson and Clark 1992b, Bond and Jones 2009). Values of $\delta^{15}N$ are also influenced by the nutritional status of the bird (Sears et al. 2008) as well as the isotopic value at the base of the food web that can vary considerably among habitats with different sources of nitrogen and different ecosystem processes. Caution must be taken, therefore, when interpreting $\delta^{15}N$ in terms of trophic position without prior knowledge of $\delta^{15}N$ signatures at the base of the food web (Post 2002). For this reason, we have reported and discussed $\delta^{15}N$ values, but only draw very conservative conclusions regarding relative trophic position, as baseline $\delta^{15}N$ information was unknown. The final stable isotope used in this study, $\delta^{34}S$, is highly influenced by whether sulfur fixation occurred in freshwater or marine environments (Lott et al. 2003) and is therefore useful in identifying the extent of marine versus freshwater resources use.

Further caution must be taken when comparing isotope values among multiple species because, as a consumer assimilates dietary nutrients into its own tissues, the isotopic values of those tissues may deviate from that observed in the original diet. This diet-tissue discrimination varies among species (Caut et al. 2009) such that, without the correct discrimination factor for

specific species and tissues, comparisons among species are subject to this potential error (Bond and Diamond 2011). We only considered inter-specific isotopic differences greater than the standard deviation of discrimination factors of bird feathers (approximately 1.5‰ for carbon and 1.1‰ for nitrogen; Caut et al. 2009) to reflect differences in diet and foraging behavior among species.

The objectives of this study were to examine foraging habitat use of a suite of waterbird species nesting within the harbor, and to identify the habitats that were particularly important among waterbird populations and across regions. We expected to find variation in waterbird foraging behavior based on differences in the general foraging strategies among species and on habitat availability near their nesting locations. In particular, we predicted that: 1) cormorants would have the highest correlation between nearby habitat availability and habitat use, as these birds can dive for prey in waters immediately surrounding their nesting habitats; 2) we expected to see broader resource use and larger isotopic niche size in long-legged wading birds, particularly on islands that lacked shorelines with suitably shallow foraging habitat; and 3) we anticipated gulls to exhibit the largest isotopic niche size, as these birds are known to be primarily generalist scavengers.

Methods

Study Area

This study was conducted across five islands in the harbor (Figure 2.1): two in Lower New York Bay (Hoffman and Swinburne islands), one in the East River (South Brother Island), and two in Jamaica Bay (Canarsie Pol and Elder's Point Marsh). These three focal regions (Lower New York Bay, the East River, and Jamaica Bay) were chosen because they contain the

three largest and most diverse waterbird colonies in the harbor, and because they encompass a variety of aquatic habitat types ranging from brackish and freshwater tributaries to marine. Public access to all islands is restricted for the protection of waterbirds.

Hoffman and Swinburne are man-made islands located off the east shore of Staten Island, New York (40° 34' 43.38" N, 74° 3' 13.51" W) in Lower New York Bay. These islands are part of the National Park Service's Gateway National Recreation Area. Aquatic habitat in Lower New York Bay is primarily marine, as the bay opens onto the Atlantic Ocean. South Brother Island (40° 47' 46.00" N, 73° 53' 53.02" W) is a natural island situated between Riker's Island and the Bronx, New York. This island is owned by the New York City Department of Parks and Recreation. Aquatic habitat near South Brother Island ranges from brackish to freshwater. Canarsie Pol (40° 37' 16.03" N, 73° 52' 23.88" W) and Elder's Point Marsh (40° 38' 9.97" N, 73° 50' 55.50" W) are natural islands situated in the northwest region of Jamaica Bay, and are both part of the National Park Service's Gateway National Recreation Area. As in Lower New York Bay, aquatic habitat in Jamaica Bay is primarily marine, as the bay opens onto the Atlantic Ocean.
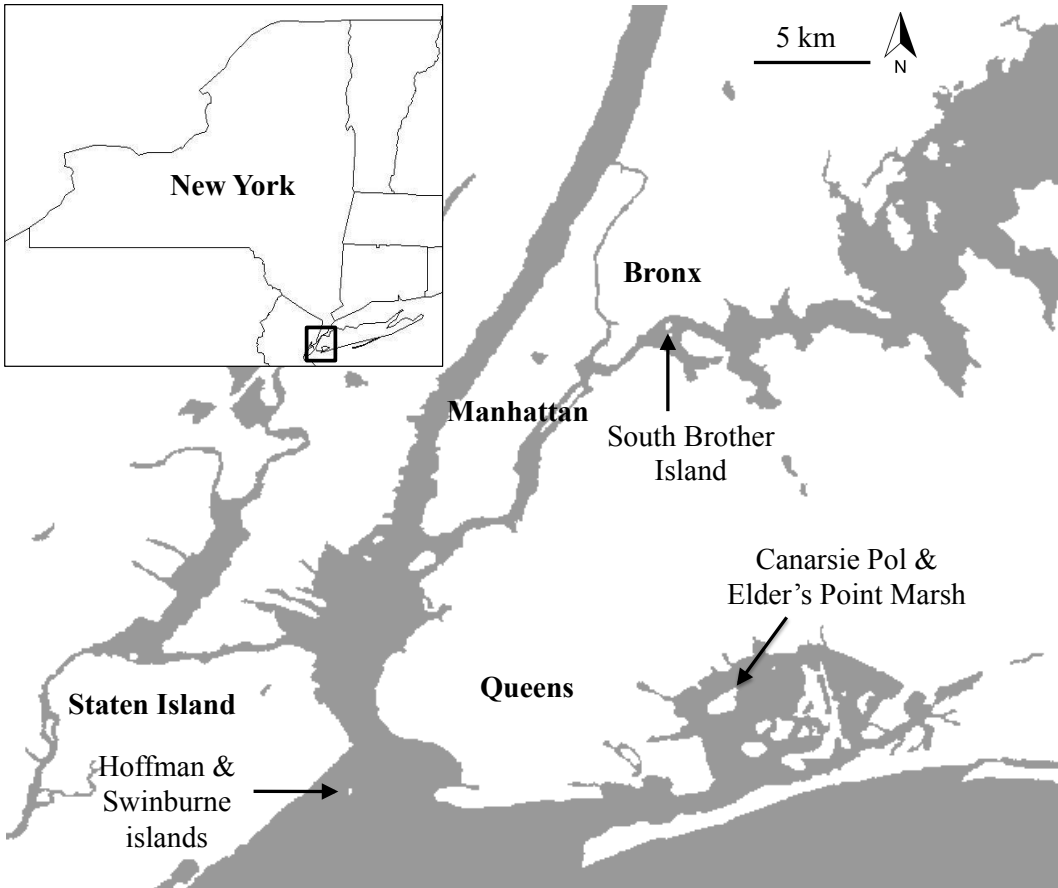
Figure 2.1. Map of the New York Harbor estuary indicating locations where feather samples were collected: Lower New York Bay (Hoffman and Swinburne islands), East River (South Brother Island), and Jamaica Bay (Canarsie Pol and Elder's Point Marsh).

Focal Species

Six waterbird species were chosen as focal species in this study. These included three long-legged wading birds (Black-crowned Night-Heron, *Nycticorax nycticorax*, hereafter night-heron; Glossy Ibis, *Plegadis falcinellus*, hereafter ibis; and Great Egret, *Ardea alba*, hereafter egret), one diving bird (Double-crested Cormorant, *Phalacrocorax auritus*, hereafter cormorant), and two gulls (Great Black-backed Gull, *Larus marinus*; and Herring Gull, *L. argentatus*). These six species were the most numerically abundant waterbirds nesting in the harbor during this study, and were selected to span the range in phylogeny, conservation status, and foraging

21

strategy within the waterbird community. In general, long-legged wading birds (ibises, egrets, and night-herons) capture fish, crabs, amphibians, and aquatic invertebrates by wading into shallow waters and marshes (Davis and Kricher 2000, McCrimmon et al. 2001, Hothem et al. 2010), cormorants dive to capture prey (primarily fish; Hatch and Weseloh 1999), and gulls scavenge for a variety of items ranging from fish to human garbage (Pierotti and Good 1994, Good 1998).

Feather Collection

In June and July, from 2009 to 2012, waterbird nestlings of each species were captured by hand at nesting colonies in coordination with permitted studies and banding programs conducted by the New York City Audubon Society. Between one and 10 contour feathers per individual were collected while the nestlings were handled for banding. In addition, between June and September of each year, contour feathers were collected from recently deceased waterbird nestlings of known species identity encountered on each island. All feather samples were stored in labeled paper envelopes and classified by species and location (Table 4.1).

Stable Isotope Analysis

All feather samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$. A 1-mg sample ($\pm$ 0.1 mg) of each feather was encapsulated in tin and analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Thermo Finnigan Delta V Advantage isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyzer (EA) at Cornell University's Stable Isotope laboratory. An internal laboratory standard of mink tissue was analyzed for every ten unknowns. A chemical methionine standard was used to measure instrumental accuracy across a gradient of amplitude intensities. Isotope corrections

were performed using a two-point normalization (linear regression) of all raw $\delta^{13}C$ and $\delta^{15}N$ data with two additional in-house standards: Cayuga Lake brown trout and corn. Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be $\pm 0.2‰$ for $\delta^{13}C$, and $\pm 0.3‰$ for $\delta^{15}N$.

A subset of Herring Gull samples was also analyzed for $\delta^{34}S$ to explore the potential for anthropogenic contributions to diet. For these individuals, a 1-mg sample (± 0.1 mg) of each feather was encapsulated in tin and analyzed for $\delta^{34}S$ at the University of Utah's Stable Isotope Ratio Facility for Environmental Research using EA-IRMS. Internal laboratory standards were analyzed for every ten unknowns. Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be $\pm 0.3‰$ for $\delta^{34}S$.

Statistical Analysis

Single-factor multivariate analysis of variance (MANOVA) and post-hoc analysis of variance (ANOVA) with Tukey-Kramer HSD were used to determine statistically significant variation in $\delta^{13}C$ and $\delta^{15}N$ values using a factor of nesting location or species depending on the analysis. A MANOVA of $\delta^{13}C$ and $\delta^{15}N$ was conducted using either mortality or year (by species) as the single factor to confirm that isotope values did not differ significantly between live and dead birds (as in Vasil et al. 2012) or across sampling years. The $\delta^{13}C$ and $\delta^{15}N$ values of feathers collected from live versus dead nestlings, and across multiple years were not found to differ significantly ($p > 0.05$), therefore the data were analyzed regardless of mortality or collection year for all subsequent analyses. These statistical analyses were performed using JMP statistical software (SAS Institute 2013).

Isotopic niche size ($‰^2$) of each waterbird population was calculated with the SIAR package in R (R Development Core Team 2014) using a Bayesian approach to estimate standard

ellipse area (SEA$_B$) of the δ^{13}C and δ^{15}N data (Jackson et al. 2011). This approach was chosen as it is well suited for small sample sizes, and it provides a measure of uncertainty around the estimated isotopic niche size allowing for statistical comparisons. The number of posterior draws in the model was set at 10^6.

Results

The waterbird community exhibited both inter- and intra-specific variation in δ^{13}C and δ^{15}N (whole MANOVA model: $F_{8,277}=38.25$, $p < 0.001$). For each species discussed below, isotopic values are reported as mean $\pm$ SD of δ^{13}C and δ^{15}N (Table 2.1), and isotopic niche sizes are reported as the mode of the SEA$_B$ posterior distribution (Figure 2.2).
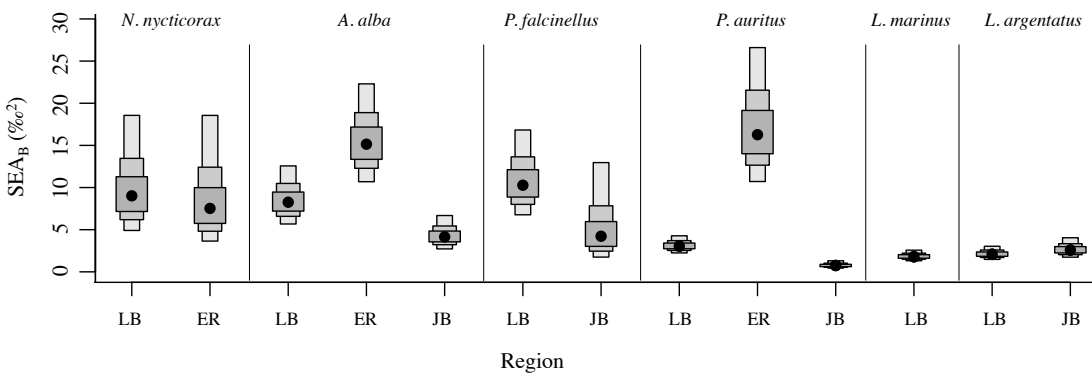
Figure 2.2. Density plot showing Bayesian estimates of the posterior distributions of isotopic niche size (SEA$_B$) with 50, 75 and 95% credible intervals in shaded boxes, and mode values of SEA$_B$ indicated by black dots. Data for each species (Black-crowned Night-Heron, *Nycticorax nycticorax*; Great Egret, *Ardea alba;* Glossy Ibis, *Plegadis falcinellus;* Double-crested Cormorant, *Phalacrocorax auritus*; Great Black-backed Gull, *Larus marinus*; and Herring Gull, *Larus argentatus*) are divided into focal regions: Lower New York Bay (LB), East River (ER) and Jamaica Bay (JB).

Table 2.1. Mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values and sample sizes (n) of feathers sampled from colonial waterbird nestlings of six species (Black-crowned Night-Heron, *Nycticorax nycticorax*; Great Egret, *Ardea alba;* Glossy Ibis, *Plegadis falcinellus;* Double-crested Cormorant, *Phalacrocorax auritus;* Great Black-backed Gull, *Larus marinus*; and Herring Gull, *Larus argentatus*) in three regions of the New York Harbor estuary (Lower New York Bay, East River, and Jamaica Bay) from June to September 2009-2012. Locations with different letters in parentheses represent significant intraspecific differences according to Tukey-Kramer HSD. n.s.: not significant

Species	Region	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	HSD
N. nycticorax	Lower New York Bay	9	-18.9 ± 1.9	14.7 ± 2.1	(a)
	East River	6	-20.9 ± 3.4	14.3 ± 1.2	(a)
					n.s.
A. alba	Lower New York Bay	25	-20.2 ± 2.2	14.4 ± 1.7	(a)
	East River	29	-20.7 ± 2.9	14.8 ± 2.1	(a)
	Jamaica Bay	20	-15.4 ± 1.8	15.3 ± 0.8	(b)
					$p < 0.001$
P. falcinellus	Lower New York Bay	19	-24.7 ± 2.1	8.0 ± 2.1	(a)
	Jamaica Bay	4	-18.4 ± 2.5	10.5 ± 1.6	(b)
					$p < 0.001$
P. auritus	Lower New York Bay	39	-16.5 ± 1.3	15.6 ± 1.0	(a)
	East River	19	-20.5 ± 3.8	15.0 ± 1.7	(b)
	Jamaica Bay	16	-14.5 ± 0.3	15.6 ± 0.6	(c)
					$p < 0.001$
L. marinus	Lower New York Bay	37	-16.7 ± 0.5	15.9 ± 1.2	
L. argentatus	Lower New York Bay	32	-17.3 ± 0.7	12.8 ± 1.3	(a)
	Jamaica Bay	23	-17.1 ± 0.7	12.7 ± 1.3	(a)
					n.s.

Of the three long-legged wading birds sampled in this study, only the night-herons did not exhibit regional isotopic variation. Average $\delta^{15}N$ values were relatively high (14.3 ± 1.2‰ and 14.7 ± 2.1‰; Table 2.1) in both sampled regions, Lower New York Bay and the East River. Average $\delta^{13}C$ values were also regionally similar, and the range in $\delta^{13}C$ (from -25.8‰ to -14.8‰) suggested a broad mix of resource use from freshwater/brackish and marine habitats. Night-herons foraged in a moderate-sized isotopic niche in comparison to other long-legged wading birds, (9.3‰^{2} in Lower New York Bay and 7.7‰^{2} in the East River), and exhibited no significant regional variation in isotopic niche size (Figure 2.2)

The other two long-legged wading birds, egrets and ibises, both exhibited regional variation in isotope values ($p < 0.001$ for both species). Similar to night-herons, egrets from Lower New York Bay and the East River had relatively high average $\delta^{15}N$ values (14.4 ± 1.7‰ to 14.8 ± 2.1‰; Table 2.1), and a similar range of $\delta^{13}C$ values (from -25.3‰ to -13.7‰) with little regional variation. However, egrets sampled from Jamaica Bay exhibited higher $\delta^{13}C$ values on average (Table 2.1), and ranged from -19.6‰ to -13.3‰, indicating a greater proportion of marine resource use. Unlike night-herons, egrets also showed significant regional variation in isotopic niche size (Figure 2.2), with a relatively large isotopic niche in the East River (15.4‰^{2}), an intermediate-sized isotopic niche in Lower New York Bay (8.6‰^{2}; smaller than the East River; $p = 0.01$) and a small isotopic niche in Jamaica Bay (4.3‰^{2}, smaller than Lower New York Bay; $p = 0.01$; Figure 2.2).

Ibises were sampled in Lower New York Bay and Jamaica Bay (they did not nest in the East River during the sampling period), and exhibited isotopic variation between these regions ($p < 0.001$). Ibises had relatively lower $\delta^{15}N$ values in both regions (8.0 ± 2.1‰ to 10.5 ± 1.6‰), and in fact, exhibited the lowest $\delta^{15}N$ values of the six focal species in this study. While ibises

sampled from Jamaica Bay had $\delta^{13}C$ values within the range observed in other long-legged

wading birds (from -20.9‰ to -16.1‰), the values observed in Lower New York Bay (ranging

from -27.4‰ to -19.2‰) were significantly lower on average (-24.7 ± 2.1‰; $p < 0.001$; Table

2.1) indicating a greater proportion of freshwater resource use. The isotopic niche size of ibises

exhibited no regional variation, with a moderate-sized isotopic niche in Lower New York Bay

($10.4‰^2$) and in Jamaica Bay ($4.4‰^2$; Figure 2.2).

Cormorants exhibited isotopic variation among all three focal regions ($p < 0.001$; Table

2.1). Relatively high $\delta^{13}C$ values were observed in birds from Jamaica Bay (from -15.1‰ to -

14.2‰), indicative of a predominantly marine diet. Cormorants from Lower New York Bay had

a broader $\delta^{13}C$ range (from -22.1‰ to -15.2‰) similar to that observed in the night-herons and

egrets from this region. East River cormorants exhibited an even broader range (from -28.3‰ to

-15.6‰) and lower average $\delta^{13}C$ value (-20.5 ± 3.8‰; Table 2.1), suggesting a greater

contribution of freshwater resources than observed in the other two regions. Average $\delta^{15}N$ values

were relatively high (from 15.0 ± 1.7‰ to 15.6 ± 1.0‰; Table 2.1) and similar among regions.

As observed in egrets, the cormorants nesting in the East River had a larger isotopic niche

($16.7‰^2$; $p < 0.001$) than those observed in the other two nesting regions ($3.2‰^2$ in Lower New

York Bay and $0.8‰^2$ in Jamaica Bay). The isotopic niche size in Lower New York Bay was in

turn larger than that observed in Jamaica Bay ($p < 0.0001$), although by a far narrower margin

(Figure 2.2).

The Great Black-backed Gull was only sampled in one location (Lower New York Bay),

while the Herring Gull was sampled in Lower New York Bay and Jamaica Bay. Great Black-

backed Gulls exhibited the highest average $\delta^{15}N$ value observed in this study (15.9 ± 1.2‰;

Table 2.1). The $\delta^{13}C$ values were also relatively high (ranging from -17.6‰ to -15.9‰)

indicating a predominantly marine diet. Interestingly, despite its reputation as a generalist scavenger, this species exhibited a very small isotopic niche ($1.9‰^2$). The second gull species, the Herring Gull, showed no regional isotopic variation. It had lower average δ^{15}N values than the Great Black-backed Gull ($12.7 \pm 1.3‰$ and $12.8 \pm 1.3‰$; Table 2.1), but similar δ^{13}C values (ranging from $-19.1‰$ to $-15.8‰$). Sulfur SIA was conducted on a subset of Herring Gull feathers (n=5) from Jamaica Bay and Lower New York Bay to investigate potential anthropogenic resource use. SIA yielded an average δ^{34}S value of $10.0 \pm 2.1‰$; a lower value than would be expected in a marine-foraging bird (Lott et al. 2003). Interestingly, Herring Gulls also had a very small isotopic niche ($2.2‰^2$ in Lower New York Bay and $2.7‰^2$ in Jamaica Bay), with no regional variation (Figure 2.2).

Discussion

The stable isotope approach used in this study allowed us to evaluate differences in foraging ecology among species nesting in three regions of the harbor, and identify the habitat types that were most important in the diet of individual populations within this urban estuary. As generally predicted, waterbird populations exhibited both inter- and intra-specific variation in δ^{13}C and δ^{15}N, indicating differences in foraging habitat use among regions and species. While it is not surprising to find differences in isotopic values among species with differing foraging ecologies, this variation suggests, depending on the species- and region-specific conservation goal, management strategies would potentially need to target very different foraging habitats for protection and remediation.

Only two of our three original hypotheses were supported. Our first hypothesis was that cormorant habitat use would reflect the foraging habitat types in the vicinity of each colony.

Cormorants from Lower New York Bay and Jamaica Bay had δ^{13}C values indicative of a predominantly marine diet, and suggested that birds likely foraged in the bays surrounding their respective nesting colonies, as well as the coastal Atlantic Ocean. Cormorants from the East River exhibited a lower average δ^{13}C value, indicating a greater contribution of freshwater resources than observed in the other two regions. This is consistent with the brackish/freshwater environment surrounding the East River colony. Cormorants nesting in the East River also exhibited a larger isotopic niche than those observed in the other two nesting regions (five times the range observed in Lower New York Bay, and 20 times that observed in Jamaica Bay), indicating that a wider range of foraging habitats and prey items contributed to the diet of these birds. This observation may reflect the diverse nature of foraging habitat availability in the East River and its freshwater tributaries. Alternatively, birds nesting at this location might have foraged at greater distances from the colony to meet their metabolic needs and those of their young, as the area surrounding this colony is highly developed. The resulting increased foraging distance would also explain the large range of δ^{13}C values (the largest range observed in this study).

The second hypothesis was that long-legged wading birds would exhibit broader resource use and have larger isotopic niches. This hypothesis was driven by the fact that the nesting islands used by wading birds, particularly the man-made islands in Lower New York Bay, provided little suitable shallow foraging habitat. Night-herons met this prediction, as they exhibited a large range in δ^{13}C values and relatively large isotopic niches in both Lower New York Bay and the East River. As long-legged wading birds, their foraging strategy may have required them to forage at greater distances from their colony sites, exposing them to a large and overlapping range of foraging habitats.

In contrast to night-herons, egrets had a significantly larger isotopic niche in the East River than in Lower New York Bay. The isotopic niche size was likely influenced by the same factors proposed for cormorants. Egrets in Jamaica Bay exhibited very high $\delta^{13}C$ values suggesting a primarily marine diet. Together with a small isotopic niche, the data suggest that egrets nesting in Jamaica Bay likely also foraged in Jamaica Bay. This conclusion is supported by the presence of extensive suitable saltwater marsh and sandy beach habitat in this region.

The final long-legged wading bird, the ibis, exhibited a similar pattern in Jamaica Bay, with $\delta^{13}C$ values suggesting a primarily marine diet, and a relatively small isotopic niche, together indicating that these birds likely remained in Jamaica Bay to forage. Ibises in Lower New York Bay exhibited significantly lower $\delta^{13}C$ values, indicating that despite the absence of freshwater resources surrounding their nesting colony, freshwater foraging habitats were the most important habitat type for this population during chick rearing. Their use of freshwater resources to feed their growing nestlings is consistent with studies conducted on White Ibis in Florida (Bildstein 1993). It is not surprising that ibises from Lower New York Bay would travel some distance from their nesting colony to forage, as the nesting islands in this region are man made with steep stone shorelines unsuited for the ibis foraging strategy. The observation that ibises from Lower New York Bay and Jamaica Bay used vastly different foraging habitat types and prey base is novel, and has not been suggested by observational methods. Ibises from both regions exhibited the lowest $\delta^{15}N$ values of the six focal species in this study. These low $\delta^{15}N$ values might have derived from a difference in source nitrogen in foraging habitats used by ibises, but most likely indicated that these birds generally relied on prey of a low relative trophic position. This is supported by the general foraging strategy of ibises, which, unlike egrets and night-herons, tend to forage by probing for invertebrates in shallow water, fields, and marshes

(Davis and Kricher 2000).

The third hypothesis, that gull species would exhibit the largest isotopic niches as generalist scavengers, was not supported by our analysis. In fact the exact opposite was observed: gulls had among the smallest isotopic niches in this study. Interestingly, the Great Black-backed Gulls observed in Lower New York Bay exhibited $\delta^{13}C$ and $\delta^{15}N$ values very similar to those observed in cormorants in the same region (Table 2.1). The general understanding of the foraging strategies of cormorants (diving predators) and gulls (generalist scavengers) does not explain this similarity. Great Black-backed Gulls, however, have been known to exhibit predatory behavior (Good 1998), and were observed during this study consuming cormorant eggs and young when the cormorant colonies were disturbed. While it is possible that these species were eating different food sources with the same isotope value, we hypothesize that the similarity was due to gulls consuming a combination of cormorant eggs and young, and scavenging for food scraps in the understory beneath the cormorant colony. Regardless of the specific scavenging or predatory behavior, our results suggest that cormorant-related diet items may be the most important food source for Great Black-backed Gulls nesting in Lower New York Bay. This specialized diet would explain the small isotopic niche observed in this species.

Herring Gulls sampled in both Lower New York Bay and Jamaica Bay exhibited relatively high $\delta^{13}C$ values (similar to those observed in the Great Black-backed Gull) but relatively low $\delta^{15}N$ values (Table 2.1). These $\delta^{15}N$ values might be explained by the scavenging of fish from lower trophic positions in a marine environment, although there is no simple mechanism for a generalist scavenger to specialize in lower trophic position carrion. This hypothesis was further undermined by sulfur SIA for a subset of Herring Gull feathers, that

31

yielded an average $\delta^{34}S$ value lower than would be expected in a marine-foraging bird (Lott et al.

2003). The most likely explanation for the isotopic values observed in Herring Gulls is

anthropogenic resource use. Scavenging of human food waste could lead to the observed high

$\delta^{13}C$ values through the consumption of C_4 photosynthetic plant materials such as corn- and cane

sugar-based foods, as well as the relatively low $\delta^{34}S$ values due to the use of fresh water in

agriculture. Such resource use could also lead to the lower observed $\delta^{15}N$ values due to the

relatively low trophic position of these diet items. The distribution of isotope values in Herring

Gulls from Lower New York Bay and Jamaica Bay overlapped to an extent not observed in any

other focal species suggesting that Herring Gulls exhibited little to no regional variation in

foraging habitat use. With the additional evidence of small isotopic niche, suggesting limited

variation in the diet, we conclude that anthropogenic foods were likely the primary resource used

by Herring Gulls provisioning their young in both nesting regions sampled in this study.

Overall, SIA of nestling feathers provided novel information about the foraging resources

that were most important to waterbirds in regions across the harbor, and should be used in the

identification and prioritization of foraging habitats based on their importance to species of

conservation concern. However, SIA alone cannot clearly distinguish among multiple foraging

sites where similar foraging habitat types are available. Monitoring and tracking methods such as

radio- and satellite-telemetry can provide information about physical locations frequented by

individuals of a population, and can be used to compile the suite of sites for potential protection

or remediation. SIA can then be used to prioritize foraging habitats based on the relative

importance of the resources they provide, and also to modify and focus monitoring efforts on

habitat types known to be of particular importance to a focal population. An integrative approach

of observational methods and SIA will therefore facilitate both the identification of a suite of

potential foraging sites, and the prioritization of those sites for waterbird conservation.

REFERENCES

Bearhop, S., D. Thompson, S. Waldron, I. Russell, G. Alexander, and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. Journal of Applied Ecology 36:75–84.

Bildstein, K. L. 1993. White Ibis, wetland wanderer. Smithsonian Institution Press, Blue Ridge Summit, PA.

Bond, A. L., and A. W. Diamond. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecological Applications 21:1017–1023.

Bond, A., and I. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. Marine Ornithology 37:183–188.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

Cherel, Y., K. A. Hobson, and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122:155–162.

Davis, W. E. and J. Kricher. 2000. Glossy Ibis (*Plegadis falcinellus*). No. 74 *in* A. Poole editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40:503–537.

Good, T. P. 1998. Great Black-backed Gull (*Larus marinus*). No. 330 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Harbor Herons Subcommittee. 2010. The Harbor Herons Conservation Plan- New York/New Jersey Harbor Region. S. B. Elbin and N. K. Tsipoura, editors. NY-NJ Harbor Estuary Program, New York, NY, USA.

Hatch, J. J. and D. V. C. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). No. 441 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hebert, C. E., D. V. C. Weseloh, A. Idrissi, M. T. Arts, and E. Roseman. 2009. Diets of aquatic birds reflect changes in the Lake Huron ecosystem. Aquatic Ecosystem Health & Management 12:37–44.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326.

Hobson, K. A., and R. G. Clark. 1992*a*. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94:181–188.

Hobson, K. A., and R. G. Clark. 1992*b*. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189–197.

Hothem, L. R., B. E. Brussee and W. E. Davis. 2010. Black-crowned Night-Heron (*Nyctocorax nycticorax*). No. 74 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

Kushlan, J. A. 2012. A history of conserving colonial waterbirds in the United States. Waterbirds 35:608–625.

Lott, C. A., T. Meehan, and J. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. Oecologia 134:505–510.

McCrimmon Jr., D. A., J. C. Ogden, and G. T. Bancroft. 2001. Great Egret (*Ardea alba*). No. 570 *in* A. Poole editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Mizutani, H., M. Fukuda, Y. Kabaya, and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk 107:400–403.

Newsome, S. D., C. Martínez del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429–436.

Parnell, J. F., D. G. Ainley, H. Blokpoel, B. Cain, T. W. Custer, J. L. Dusi, S. Kress, J. A. Kushlan, W. E. Southern, and L. E. Stenzel. 1988. Colonial waterbird management in North America. Colonial Waterbirds 11:129–169.

Pierotti, R. and T. P. Good. 1994. Herring Gull (*Larus argentatus*). No. 124 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

R Development Core Team 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Downloaded September 2014.

SAS Institute. 2013. JMP statistical discovery software. Eleventh edition. SAS institute, Cary, NC.

Sears, J., S. A. Hatch, and D. M. O'Brien. 2008. Disentangling effects of growth and nutritional status on seabird stable isotope ratios. Oecologia 159:41–48.

Steele, K. W., and R. M. Daniel. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. Journal of Agricultural Science 90:7–9.

Vasil, C. A., M. J. Polito, W. P. Patterson, and S. D. Emslie. 2012. Wanted: dead or alive? Isotopic analysis (δ13C and δ15N) of *Pygoscelis* penguin chick tissues supports opportunistic sampling. Rapid Communications in Mass Spectrometry 26:487–493.

CHAPTER 3

ISOTOPIC DISCRIMINATION IN THE DOUBLE-CRESTED CORMORANT
(*PHALACROCORAX AURITUS*)

Elizabeth Craig[1], Brian Dorr[2], Katie Hanson-Dorr[2], Jed Sparks[3], Paul Curtis[4]

[1] Field of Zoology and Wildlife Conservation,
Cornell University, Ithaca, NY, 14853, USA

[2] United States Department of Agriculture, Wildlife Services, National Wildlife Research Center,
Mississippi Field Station, Mississippi State, MS 39762, USA

[3] Department of Ecology and Evolutionary Biology,
Cornell University, Ithaca, NY, 14853, USA

[4] Department of Natural Resources,
Cornell University, Ithaca, NY, 14853, USA

Abstract

The diet-tissue discrimination factor is the amount by which a consumer's tissue varies isotopically from its diet, and is therefore a key element in models that use stable isotopes to estimate diet composition. In this study we measured discrimination factors in blood (whole blood, red blood cells and plasma), liver, muscle and feathers of Double-crested Cormorants (*Phalacrocorax auritus*) for stable isotope ratios of carbon, nitrogen and sulfur. Cormorants exhibited discrimination factors that differed significantly among tissue types (for carbon and nitrogen), and differed substantially (in the context of the isotopic variation among relevant prey species) from those observed in congeneric species. The Double-crested Cormorant has undergone rapid population expansion throughout much of its historic range over the past three decades leading to both real and perceived conflicts with fisheries throughout North America, and this study provides an essential link for the use of stable isotope analysis in researching foraging ecology, diet, and resource use of this widespread and controversial species.

Introduction

The use of stable isotope analysis (SIA) has become widespread in studies of wildlife diet and foraging ecology, as the isotopic value observed in the tissue of an animal reflects that of its diet (DeNiro and Epstein 1978, Inger and Bearhop 2008). However, as a consumer assimilates dietary nutrients into its own tissues, the isotopic values of those tissues may deviate from that observed in the original diet; a process called isotopic discrimination. The isotopic value observed in the tissue of a consumer (δX_t) is equivalent to the isotopic value of its diet (δX_d) plus the diet-tissue discrimination factor ($\varDelta X$): $\delta X_t = \delta X_d + \varDelta X$ (equation 1), where X is the stable isotope of interest (e.g., ^{13}C, ^{15}N, or ^{34}S). If we know $\varDelta X$ and can measure δX_t, we can solve for

39

δX_d, revealing information about the animal's diet and foraging behavior. Discrimination factors vary among species and among tissue types within a species (Hobson and Clark 1992*a*, Caut et al. 2009) such that, without the correct species- and tissue-specific discrimination factor, meaningful inferences about diet and foraging ecology cannot be made.

Stable isotope values are discussed here using delta notation: $\delta X = (R_{sample} - R_{standard})/R_{standard}) \times 1000$ (equation 2), where X is, for example, ^{13}C, ^{15}N or ^{34}S, and R is the corresponding ratio of heavy to light isotopes (e.g., $^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$) in either the sample of interest (R_{sample}) or an international reference standard ($R_{standard}$). Stable isotope ratios, including $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$, have proven useful in identifying diet and resource use in wild animals. $\delta^{13}C$ is used in diet studies as an indication of the animal's foraging environment as it is highly influenced by the type of photosynthesis by which carbon is fixed (i.e., C_3, C_4 or CAM photosynthesis) as well as the source of carbon and the photosynthetic environment (terrestrial, aquatic, pelagic, benthic, etc.; (Farquhar et al. 1989, France 1995, Rubenstein and Hobson 2004). $\delta^{13}C$ tends not to change substantially with trophic exchange (i.e., little to no $\Delta^{13}C$), and for this reason, information about primary production is largely preserved in $\delta^{13}C$ values throughout the food web (DeNiro and Epstein 1978). This small $\Delta^{13}C$ may be due to carbon isotopic fractionation during assimilation or respiration (Peterson and Fry 1987). Researchers have observed $\Delta^{13}C$ in a variety of aquatic and terrestrial food webs, and reported a range of $\Delta^{13}C$ from -3 to 4‰, with averages of 0.2‰ (Peterson and Fry 1987), 0.4‰ (Post 2002), 0.75‰ (Caut et al. 2009) and the commonly cited 1‰ (DeNiro and Epstein 1978).

$\delta^{15}N$ is often used in examining trophic dynamics within food webs as it exhibits significant $\Delta^{15}N$ with trophic exchange, which can be used as an indicator of relative trophic position (Bond and Jones 2009). $\Delta^{15}N$ is generally positive, and is largely attributed to the

excretion of isotopically lighter nitrogen in urine (or urate in the case of birds), leaving the isotopically heavier nitrogen within the consumer's system to be assimilated through tissue growth. As with $\Delta^{13}C$, researchers have observed $\Delta^{15}N$ in a variety of aquatic and terrestrial food webs, and reported a range of $\Delta^{15}N$ from -1 to 10‰, with averages of 3.2‰ (Peterson and Fry 1987), 3.4‰ (Post 2002) and 2.75‰ (Caut et al. 2009).

$\delta^{34}S$ is highly influenced by whether sulfur fixation occurred in freshwater or marine environments (Lott et al. 2003), and, like $\Delta^{13}C$, exhibits little to no $\Delta^{34}S$ with trophic exchange, preserving information about the source of sulfur throughout the food web. $\Delta^{34}S$ has been observed to range from -1 to 2‰, with an average of 0.2‰ (Peterson and Fry 1987). The major dietary source of sulfur is in essential amino acids such as cysteine and methionine, which are generally limited in animal diets and therefore are not often considered to have potential for discrimination (Hesslein et al. 1991, Hebert et al. 2008).

Isotopic mixing models are increasingly used to identify diet composition (when components of the diet are isotopically distinct (Phillips 2001). Because discrimination factors are unknown for most organisms, assumptions about the magnitude and direction of discrimination must often be made for these model approaches. However, slight differences in discrimination factors can lead to meaningful differences in the model estimate of diet composition (Ben-David and Schell 2001, Bond and Diamond 2011), and the predictive strength of these models therefore increases greatly if the species- and tissue-specific discrimination factors are known.

In this study we identify $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ in the Double-crested Cormorant (*Phalacrocorax auritus*). The Double-crested Cormorant is a piscivorous colonial waterbird native to North America (Hatch and Weseloh 1999). Over the past three decades this species has

undergone rapid population expansion throughout much of its historic range (Hatch 1995, Hatch and Weseloh 1999, Wires and Cuthbert 2006), leading to both real and perceived conflicts with fisheries throughout North America (Glahn et al. 2002, Taylor and Dorr 2003, Rudstam et al. 2004, Diana et al. 2006, Dorr et al. 2012*a*, *b*). Rising interest in the diet and foraging behavior of this species has led investigators to seek new methods of evaluating cormorant resource use. Studies have recently begun to employ SIA to this end (Hobson et al. 1997, Hebert et al. 2008, 2009, Hobson 2009, Doucette et al. 2010, 2011, Ofukany et al. 2012). This study provides an essential link for the use of SIA in researching foraging ecology, diet and resource use of this widespread and controversial species.

Materials and methods

This research was conducted under the approval of the US Department of Agriculture, Wildlife Services, National Wildlife Research Center's (NWRC) Institutional Animal Care and Use Committee (protocol QA-1723). Six wild cormorants (all male) were captured at night roosts in Lubbub Creek, Alabama, and Bluff Lake, Mississippi (MS) between 14 and 21 January 2010. These birds were transported to the captive waterbird facility at the NWRC Field Station in Starkville, MS. Cormorants were fed an *ad libitum* diet of farm-raised channel catfish *Ictalurus punctatus* beginning the day after capture for a period of six or eight weeks (n=3 and n=3 respectively). Cormorants were sacrificed after the allotted feeding period, allowing for the collection of liver, blood (whole blood, red blood cells and plasma) and feather (with active blood supply) samples. Samples of the catfish diet were also collected (n=22). The duration of time on the catfish diet allowed the isotopic turnover of each tissue type discussed above (Hobson and Clark 1992b, Carleton and Martínez del Rio 2005, Bauchinger and McWilliams

2009). Pectoralis muscle tissue was also collected from sacrificed birds, but as the period of the feeding trial was shorter than the typical turnover time for this tissue (four to five times that of liver; Bauchinger & McWilliams 2009), the estimates of discrimination from muscle samples were subject to this additional source of error. Muscle data are still presented here because this source of error was considered to be small as birds likely also consumed catfish prior to capture.

Stable isotope analysis

All samples were frozen and transported to Cornell University for SIA preparation. Feather samples were rinsed with deionized water and dried. Muscle and liver samples were rinsed and drained of blood. Muscle, liver, blood and catfish samples were freeze dried. Muscle, liver and catfish samples were ground to a powder using a freeze mill. Half of each ground muscle, liver and catfish sample was set aside for $\delta^{34}S$ and $\delta^{15}N$ analysis without lipid extraction. Due to the influence of lipid content on $\delta^{13}C$ in cormorant muscle and liver tissue (Doucette et al. 2010), lipids were extracted from the remainder of the cormorant muscle and liver tissues, as well as from the catfish samples, for $\delta^{13}C$ analysis. Lipids were extracted using a 2:1 chloroform:methanol solvent (Logan et al. 2008).

All non-lipid extracted samples were analyzed for $\delta^{15}N$ at the Cornell University Stable Isotope Laboratory (COIL) using a Thermo Finnigan Delta V Advantage isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyzer (EA). Feather, blood, and lipid-extracted muscle, liver and catfish samples were analyzed for $\delta^{13}C$ at COIL using EA-IRMS. All non-lipid extracted samples were analyzed for $\delta^{34}S$ at the University of Utah's Stable Isotope Ratio Facility for Environmental Research (SIRFER) using EA-IRMS. Reference standards for ^{15}N, ^{13}C and [34]S are atmospheric air, Vienna Pee Dee belemnite and Canyon Diablo troilite

43

respectively. Internal laboratory standards were analyzed for every ten unknowns. Based on

standard deviations of within-run replicate measurements of standards, analytical error was

estimated to be ±0.1‰ for δ^{13}C, ±0.4‰ for δ^{15}N and ±0.5‰ for δ^{34}S.

Statistical analysis

All statistical analyses were performed in JMP version 9.0 (SAS Institute 2013). Analysis

of variance (ANOVA) with post-hoc Tukey Kramer HSD test was used to identify differences in

discrimination factors among tissue types. Statistical analyses were considered significant at $p <$

0.05. Discrimination factors were calculated for each cormorant tissue type by solving for ΔX

using equation 1, where δX_t is the mean isotopic value in each cormorant tissue and δX_d is the

mean isotopic value of the catfish. Standard deviation for discrimination factors was calculated

by adding the standard deviation of isotopic values for each cormorant tissue type to that of the

catfish such that it accounted for both sources of variation.

Results

The catfish diet fed to cormorants in this study had an average (± one standard deviation)

δ^{13}C value of -19.1‰ (±0.8‰), δ^{15}N value of 7.6‰ (±0.5‰) and δ^{34}S value of 2.0‰ (±2.3‰).

Δ^{15}N values (Table 3.1) were all positive and generally large (ranging from 2.9 to 4.8‰). Δ^{13}C

values (Table 3.1) were smaller in magnitude (ranging from -1.1 to 0.2‰) and were

predominantly negative. Similar to Δ^{13}C, Δ^{34}S values (Table 3.1) were small in magnitude

(ranging from -1.1 to 0.5‰).

Table 3.1. Average diet-tissue discrimination factors (mean $\Delta \pm$ SD of cormorant tissue + catfish diet) for carbon, nitrogen, and sulfur stable isotopes ($\Delta^{13}C$, $\Delta^{15}N$, and $\Delta^{34}S$) in wild Double-crested Cormorants (*Phalacrocorax auritus*) fed a diet of farm-raised catfish in captivity. Tissue types that differed significantly from one another ($p < 0.05$) are indicated by different capital letters after parentheses within each column (ANOVA with post-hoc Tukey Kramer HSD).

Tissue	Discrimination factor (mean $\pm$ SD)		
	$\Delta^{13}C$ (‰)	$\Delta^{15}N$ (‰)	$\Delta^{34}S$ (‰)
Feather	0.2 $\pm$ 1.3 [A]	4.8 $\pm$ 0.8 [A]	-0.1 $\pm$ 4.1 [A]
Liver	-0.3 $\pm$ 1.1 [AB]	4.3 $\pm$ 0.5 [B]	-0.9 $\pm$ 3.8 [A]
Muscle [a]	-1.1 $\pm$ 1.2 [C]	3.9 $\pm$ 0.7 [C]	-1.1 $\pm$ 3.4 [A]
Plasma	-0.6 $\pm$ 1.1 [BC]	3.9 $\pm$ 0.7 [BC]	-0.5 $\pm$ 4.1 [A]
Red blood cells	-0.8 $\pm$ 1.1 [BC]	3.0 $\pm$ 0.6 [D]	0.1 $\pm$ 3.2 [A]
Whole blood	-1.1 $\pm$ 1.1 [C]	2.9 $\pm$ 0.6 [D]	0.5 $\pm$ 2.9 [A]

[a]Muscle tissue may not have experienced a full isotopic turnover during the captive period, however this source of error was minimized by the fact that birds likely consumed a similar diet prior to capture.

Discussion

Double-crested Cormorants exhibited discrimination factors that differed significantly among tissue types (for $\Delta^{13}C$ and $\Delta^{15}N$; Table 3.1). This was expected in light of the diversity of biochemical and physiological processes taking place within these functionally different tissues. $\Delta^{15}N$ increased significantly from tissues playing an earlier role to those playing a later role in digestion and metabolic routing. $\Delta^{15}N$ was lowest in blood samples (among which the whole blood and red blood cells were significantly lower than plasma), intermediate in liver, and highest in feathers (Table 4.1). These results are consistent with the concept that each step in a metabolic pathway results in ^{15}N enrichment (Macko et al. 1986, Vanderklift and Ponsard 2003). While both positive and negative $\Delta^{13}C$ and $\Delta^{34}S$ values were observed, all were relatively close

(within approximately 1‰) to zero. All discrimination factors observed in this study were within the range of values observed in freshwater aquatic food webs (DeNiro and Epstein 1978, Peterson and Fry 1987, Hesslein et al. 1991, Post 2002, Hebert et al. 2008, Caut et al. 2009).

Unexpectedly, Double-crested Cormorant discrimination factors differed substantially (in the context of the isotopic variation among relevant prey species) from those observed in Great Cormorants (*P. carbo*; Bearhop et al. 1999; Mizutani et al. 1992) and European Shags (*P. aristotelis*; Bearhop et al. 1999). While $\Delta^{15}N$ values observed in Double-crested Cormorant tissues were within the range observed in congeneric species, $\Delta^{13}C$ exhibited inter-specific differences in both magnitude and direction. Double-crested Cormorant $\Delta^{13}C$ values were small and primarily negative while those observed in the Great Cormorant and European Shag were larger and primarily positive (Table 3.2). Potential sources of this variation include inter-specific differences in metabolic rates or physiological processes. For instance, depending on the energy needs of the consumer, carbohydrates and fatty acids from the diet will be routed towards respiration (for immediate energy needs), fatty acid synthesis, or fat storage. Proteins from the diet are broken down, and their composite amino acids are either dissembled or, in the case of essential amino acids, used directly in protein synthesis. These biochemical and physiological processes determine the fate of nutrients consumed in the diet, and therefore play a key role in the magnitude and direction of diet-tissue discrimination.

Table 3.2. Average diet-tissue discrimination factors for carbon (Δ^{13}C) and nitrogen (Δ^{15}N) in two *Phalacrocorax* species: the Great Cormorant (*P. carbo*) and the European Shag (*P. aristotelis*).

Species	Tissue	n	Discrimination factor (mean)		Source
			Δ^{13}C (‰)	Δ^{15}N (‰)	
P. carbo					
	Feather	8	2.3	4.2	Bearhop et al. 1999
	Feather	17	3.8	3.7	Mizutani et al. 1992
	Muscle	17	1.3	2.4	Mizutani et al. 1992
	Liver	17	4.2	4.8	Mizutani et al. 1992
P. aristotelis					
	Feather	12	2.0	3.6	Bearhop et al. 1999

Conclusions

Because of their substantial differences in magnitude and direction, use of discrimination factors from different species, even congeneric species like the Great Cormorant or European Shag, to model diet in the Double-crested Cormorant would introduce substantial error into model estimates, underlining the importance of using species- and tissue-specific discrimination factors in modeling efforts.

Acknowledgements

REFERENCES

Bauchinger, U., and S. McWilliams. 2009. Carbon Turnover in Tissues of a Passerine Bird: Allometry, Isotopic Clocks, and Phenotypic Flexibility in Organ Size. Physiological and Biochemical Zoology 82:787–797.

Bearhop, S., D. Thompson, S. Waldron, I. Russell, G. Alexander, and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. Journal of Applied Ecology 36:75–84.

Ben-David, M., and D. M. Schell. 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. Oecologia 127:180–184.

Bond, A. L., and A. W. Diamond. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecological Applications 21:1017–1023.

Bond, A., and I. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. Marine Ornithology 37:183–188.

Carleton, S. A., and C. Martínez del Rio. 2005. The effect of cold-induced increased metabolic rate on the rate of ^{13}C and ^{15}N incorporation in house sparrows (*Passer domesticus*). Oecologia 144:226–232.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors ($\Delta^{15}N$ and $\Delta^{13}C$): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

DeNiro, M., and S. Epstein. 1978. Influence of diet on distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506.

Diana, J. S., S. L. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. Journal of Great Lakes Research 32:306–320.

Dorr, B. S., L. W. Burger, S. C. Barras, and K. C. Godwin. 2012*a*. Economic impact of Double-crested Cormorant, *Phalacrocorax auritus*, depredation on channel catfish, *Ictalurus punctatus*, aquaculture in Mississippi, USA. Journal of the World Aquaculture Society

43:502–513.

Dorr, B. S., S. L. Hanisch, P. H. Butchko, and D. G. Fielder. 2012b. Management of Double-crested Cormorants to improve sport fisheries in Michigan: three case studies. Human-Wildlife Interactions 6:155–168.

Doucette, J. L., B. Wissel, and C. M. Somers. 2010. Effects of lipid extraction and lipid normalization on stable carbon and nitrogen isotope ratios in Double-crested Cormorants: implications for food web studies. Waterbirds 33:273–284.

Doucette, J. L., B. Wissel, and C. M. Somers. 2011. Cormorant-fisheries conflicts: stable isotopes reveal a consistent niche for avian piscivores in diverse food webs. Ecological Applications 21:2987–3001.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40:503–537.

France, R. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnology and Oceanography 40:1310–1313.

Glahn, J., S. J. Werner, T. Hanson, and C. Engle. 2002. Cormorant depredation losses and their prevention at catfish farms: economic considerations. Human Conflicts with Wildlife: Economic Considerations Paper 17:138–146.

Hatch, J. J. 1995. Changing populations of Double-crested Cormorants. Colonial Waterbirds 18:8–24.

Hatch, J. J. and D. V. C. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). No. 441 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hebert, C. E., D. V. C. Weseloh, A. Idrissi, M. T. Arts, and E. Roseman. 2009. Diets of aquatic birds reflect changes in the Lake Huron ecosystem. Aquatic Ecosystem Health & Management 12:37–44.

Hebert, C. E., M. Bur, D. Sherman, and J. L. Shutt. 2008. Sulfur isotopes link overwinter habitat use and breeding condition in Double-crested Cormorants. Ecological Applications 18:561–567.

Hesslein, R. H., M. J. Capel, D. E. Fox, and K. A. Hallard. 1991. Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. Canadian Journal of Fisheries and Aquatic Sciences 48:2258–2265.

Hobson, K. A. 2009. Trophic interactions between cormorants and fisheries: towards a more quantitative approach using stable isotopes. Waterbirds 32:481–490.

Hobson, K. A., and R. G. Clark. 1992*a*. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189–197.

Hobson, K. A., and R. G. Clark. 1992*b*. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94:181–188.

Hobson, K. A., K. Hughes, and P. Ewins. 1997. Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. Auk 114:467–478.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

Logan, J. M., T. D. Jardine, T. J. Miller, S. E. Bunn, R. A. Cunjak, and M. E. Lutcavage. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. Journal of Animal Ecology 77:838–846.

Lott, C. A., T. Meehan, and J. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. Oecologia 134:505–510.

Macko, S. A., M. L. Fogel Estep, M. H. Engel, and P. E. Hare. 1986. Kinetic fractionation of stable nitrogen isotopes during amino acid transamination. Geochimica et Cosmochimica Acta 50:2143–2146.

Mizutani, H., M. Fukuda, and Y. Kabaya. 1992. ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. Ecology 73:1391–1395.

Ofukany, A., K. Hobson, and L. I. Wassenaar. 2012. Connecting breeding and wintering habitats of migratory piscivorous birds: implications for tracking contaminants (Hg) using multiple stable isotopes. Environmental Science & Technology 46:3253–3262.

Peterson, B., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology And Systematics 18:293–320.

Phillips, D. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 127:166–170.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology & Evolution 19:256–263.

Rudstam, L., A. VanDeValk, C. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14:149–163.

SAS Institute. 2013. JMP statistical discovery software. Eleventh edition. SAS institute, Cary, NC.

Taylor, J., and B. S. Dorr. 2003. Double-crested Cormorant impacts to commercial and natural resources. Wildlife Damage Management Conference 10:43–51.

Vanderklift, M., and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia 136:169–182.

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the Double-crested Cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. Waterbirds 29:9–37.

CHAPTER 4

USING STABLE ISOTOPES TO DECIPHER WINTER HABITAT USE OF
DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) BREEDING IN
EASTERN NORTH AMERICA

Elizabeth Craig[1], Tommy King[2], Jed Sparks[3], Paul Curtis[4]

[1] Field of Zoology and Wildlife Conservation,
Cornell University, Ithaca, NY, 14853, USA

[2] United States Department of Agriculture, Wildlife Services, National Wildlife Research Center,
Mississippi Field Station, Mississippi State, MS 39762, USA

[3] Department of Ecology and Evolutionary Biology,
Cornell University, Ithaca, NY, 14853, USA

[4] Department of Natural Resources,
Cornell University, Ithaca, NY, 14853, USA

Abstract

The Double-crested Cormorant (*Phalacrocorax auritus*) has undergone population expansion throughout much of its historic range since the 1970s, resulting in increased pressure on foraging habitats including real and perceived competition with commercial and sport fisheries and impacts on the aquaculture industry. We exploited natural variation in isotopic ratios of carbon, nitrogen, and sulfur to determine the winter habitat use (aquaculture, natural freshwater, or marine) of birds collected on their summer breeding grounds in the eastern United States (from Minnesota to Vermont). The specific objectives of this study were to: 1) determine the stable isotope ratios of birds wintering at aquaculture facilities and natural freshwater and marine habitats, and 2) determine what percent of birds at distinct breeding colonies wintered in each of these habitat types. The distribution of winter habitat type varied significantly across breeding colonies and between male and female cormorants. More specifically, use of aquaculture winter habitat was most prevalent in birds breeding in Lake Huron and Lake Erie. Overall, aquaculture habitats were used more by males, and marine habitats were used more by females. The stable isotope approach used in this study provided dietary confirmation of previously observed migratory patterns in the Double-crested Cormorant. As aquaculture resource use was found primarily in males at a broad range of breeding colonies, we suggest that targeting breeding birds in order to reduce aquaculture depredation is a less efficient strategy than managing birds at the depredation sites.

Introduction

Since the 1970s, the Double-crested Cormorant (*Phalacrocorax auritus*), a piscivorous colonial waterbird native to North America, has undergone rapid population expansion

throughout much of its historic range (Hatch 1995, Hatch and Weseloh 1999, Weseloh et al. 2002, Ridgway et al. 2006, Wires and Cuthbert 2006). Population increases have been ascribed to lower mortality due to decreased contaminant levels, reduced human persecution, and increased food sources including aquaculture (Glahn et al. 1997, Hatch and Weseloh 1999, Glahn and King 2004). Resulting cormorant abundance may place increasing pressure on foraging and nesting habitats. Cormorants can reduce habitat quality and destroy vegetation when nesting at high densities (Hebert et al. 2005, Craig et al. 2012, Kolb et al. 2012) and may compete for nesting habitat with co-occurring colonial waterbird species when nesting in mixed species colonies (Cuthbert et al. 2002, Weseloh et al. 2002, Somers et al. 2007, 2011). Cormorants have also been implicated in a range of human conflict issues including competition with commercial and sport fisheries (Taylor and Dorr 2003, Rudstam et al. 2004, Diana et al. 2006, Dorr et al. 2012b), and impacts to aquaculture facilities (e.g., Glahn et al. 2002, Glahn and King 2004, Dorr et al. 2012a). Cormorants wintering at catfish farms in the southeastern U.S. impose an annual burden of nearly $25 million through predation on fish and associated management costs (Glahn et al. 2002). Pressure from the aquaculture industry, as well as from commercial and sport fishermen, has led to increased control efforts for cormorant populations at both wintering and breeding grounds (Glahn and Stickley 1995, Glahn et al. 2000a, b, 2002, Tobin et al. 2002, Diana et al. 2006).

Studies have examined cormorant diet and foraging behavior using a variety of methods including visual observations, satellite and radio tracking, bioenergetic modeling, and stomach content, regurgitant, and pellet analysis (e.g., Glahn and Brugger 1995, King et al. 1995, Neuman et al. 1997, Glahn and Dorr 2002, Rudstam et al. 2004). These methods identify components of diet consumed at the moment of observation, but not the sum total of the animal's diet. In

contrast, stable isotope ratios including carbon (δ^{13}C), nitrogen (δ^{15}N), and sulfur (δ^{34}S) are based on the entire diet of an animal, and have therefore been recognized as highly valuable tools for assessing foraging ecology and migratory behavior in many species, including cormorants (Hobson et al. 1997, Bearhop et al. 1999, Chang et al. 2008, Hebert et al. 2008, 2009, Hobson 2009, Doucette et al. 2011, Ofukany et al. 2012). In particular, feather stable isotope values reflect a bird's diet over the timescale of feather growth, and contain information about the relative importance of foraging resources during that period (Hobson and Clark 1992*a*, *b*, Hobson 1999, Inger and Bearhop 2008, Bond and Jones 2009).

We exploited natural variation in δ^{13}C, δ^{15}N, and δ^{34}S of cormorant feathers to determine the winter resource use of birds observed at their summer breeding grounds. Specifically, we identified whether individual breeding birds previously wintered at aquaculture facilities, or natural freshwater or marine environments in the southeastern United States. Feathers grown from aquaculture resources should exhibit a unique isotopic signature based on two distinguishing characteristics of the Mississippi catfish industry (Glahn et al. 2002): 1) these facilities use freshwater ponds, and 2) the application of intensive aquaculture methods involves the use of C_4 (corn)-based fish feed. Together these characteristics should lead to relatively low δ^{34}S (Lott et al. 2003), less negative δ^{13}C (Farquhar et al. 1989), and low δ^{15}N due to the low relative trophic position of farmed fish (Steele and Daniel 1978, Minagawa and Wada 1984, Bond and Jones 2009). Feathers grown from natural freshwater resources should also exhibit low δ^{34}S, but should have more negative δ^{13}C (from their aquatic C_3-based diet; Farquhar et al. 1989), and higher δ^{15}N than feathers grown from aquaculture resources. Finally, tissues grown from marine resources should exhibit high δ^{34}S, less negative δ^{13}C (Mizutani et al. 1990, Bearhop et al. 1999), and higher δ^{15}N than feathers grown from aquaculture resources.

The specific objectives of this study were to: 1) determine the stable isotope ratios of birds wintering at aquaculture facilities and natural freshwater and marine habitats, and 2) estimate what proportion of birds at breeding colonies across eastern North America (from Minnesota to Vermont) wintered at each of these habitat types. Based on their position in the Mississippi flyway, we anticipated that breeding colonies in Lake Michigan and Lake Huron would contain a greater proportion of cormorants wintering in aquaculture habitats in comparison to colonies to the west or east (Dolbeer 1991, Hatch and Weseloh 1999, King et al. 2010, Scherr et al. 2010). While recent studies have observed cormorant movements between breeding and winter habitats (King et al. 2010, Scherr et al. 2010, Chastant et al. 2013), this study is the first to confirm winter foraging habitat use in breeding cormorants based on isotopic dietary information.

Study Area

Samples were collected at three wintering locations and five breeding locations (Figure 4.1). Winter locations included Frog Leg Lake (33.544 N, -90.291 W) in the delta region of Mississippi, USA, Lake Guntersville (34.552 N, -86.116 W) in northern Alabama, USA, and Cat Island (30.316 N, -88.206 W), in coastal Alabama, USA. These locations were chosen for their abundance of aquaculture, natural freshwater, and marine foraging habitat, respectively. Breeding locations were limited to the USA for permitting reasons, and ranged from Minnesota to Vermont, and included Wells Lake (44.291 N, -93.342 W) in southern Minnesota, USA, Garden Bay (45.780 N, -86.577 W) in northern Lake Michigan, Michigan, USA, Thunder Bay (44.999 N, -83.361 W) in western Lake Huron, Michigan, USA, Turning Point Island (41.457 N, -82.727 W) in southwest Lake Erie, Ohio, USA, and Young Island (44.740 N, -73.345 W) in

Lake Champlain, Vermont, USA. These locations were chosen to span the cormorant breeding range in eastern North America, and because each had active cormorant management programs from which culled birds could be collected.
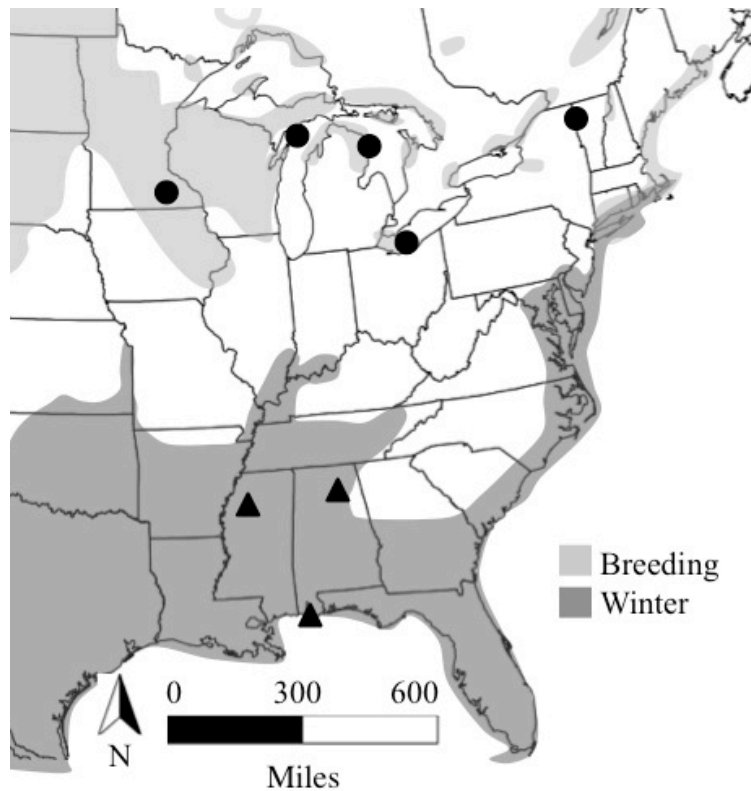
Figure 4.1. Sampling locations of Double-crested Cormorants (*Phalacrocorax auritus*) at three winter locations (triangles; Frog Leg Lake, MS; Cat Island, AL; Lake Guntersville, AL) and five breeding locations (circles; Wells Lake, MN; Lake Michigan, MI; Lake Huron, MI; Lake Erie, OH; Lake Champlain, VT) across eastern North America from 2010 to 2012 (adapted from Hatch and Weseloh 1999).

Methods

During January and February of 2011 and 2012, cormorants culled during management activities were collected from aquaculture (Frog Leg Lake; N=20), natural freshwater (Lake Guntersville; N=28), and marine (Cat Island; N=19) winter habitats. Growing flight feathers with

an active blood supply, and when present, nuptial plumes were collected from each bird and stored in paper envelopes. Both growing flight feathers and nuptial plumes were grown in late winter and therefore incorporated the bird's diet during the wintering period, as cormorants generally use the same foraging habitat type throughout this season (Scherr et al. 2010, King et al. 2012*a*).

During April and May of 2010 and 2012, cormorants culled during management activities were collected in Minnesota (N=30), Lake Michigan (N=28), Lake Huron (N=30), Lake Erie (N=30), and Lake Champlain (N=20). Nuptial plumes were collected from each bird and stored in envelopes. These nuptial plumes, like those collected on the wintering grounds, were grown in late winter and therefore incorporated the bird's diet during the wintering period. The sex of each bird was determined by dissection.

Feather samples were rinsed with deionized water and dried. All feathers were analyzed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. A 1 mg sample ($\pm$ 0.1 mg) of each feather was encapsulated in tin and analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Thermo Finnigan Delta V Advantage isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyzer (EA) at Cornell University's Stable Isotope Laboratory. An internal laboratory standard of mink tissue was analyzed for every ten feather samples. A chemical methionine standard was used to measure instrumental accuracy across a gradient of amplitude intensities. Isotope corrections were performed using a two-point normalization (linear regression) of all raw $\delta^{13}C$ and $\delta^{15}N$ data with two additional in-house standards: Cayuga Lake brown trout and corn. Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be $\pm$ 0.2‰ for $\delta^{13}C$, and $\pm$ 0.3‰ for $\delta^{15}N$. A second 1 mg sample ($\pm$ 0.1 mg) of each feather was encapsulated in tin and analyzed for $\delta^{34}S$ at the University of Utah's Stable Isotope Ratio Facility for Environmental

Research using EA-IRMS. Internal laboratory standards were analyzed for every ten feather samples. Internal laboratory standards were silver sulfide, zinc sulfide and eiderdown. Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be $\pm$ 0.3‰ for δ^{34}S.

All analyses were conducted using the statistical software package JMP (SAS Institute 2013). Isotope values of feathers from cormorants wintering in aquaculture, natural freshwater, and marine habitats were compared using an analysis of variance (ANOVA) to confirm that tissues grown in these habitats were isotopically distinct. Isotope data from wintering birds were then used to inform a discriminant analysis (Glahn and McCoy 1995) that identified the winter habitat type (aquaculture, natural freshwater, or marine) of cormorants. First, half of the data was used to inform the discriminant analysis, and the second half were used to test the accuracy of the model. As the habitat type was correctly identified in 100% of the test samples, all samples were then pooled to inform a new discriminant analysis for use in predicting winter foraging habitat type in breeding birds.

In order to confirm that nuptial plumes were representative of the foraging habitat types in which wintering birds were collected, stable isotope values of nuptial plumes and growing flight feathers (representing foraging habitat use at the time of collection) from wintering birds were entered into the discriminant model. Concurrence was observed between foraging habitat type predicted from nuptial plumes and growing flight feathers in 100% of birds.

Isotope data from breeding cormorant nuptial plumes were entered into the discriminant model to determine the foraging habitat type predominantly used during the previous winter. An exclusion threshold of 95% was applied to the posterior probability of membership (Oppel and Powell 2008) to remove individuals from the analysis that used a mix of winter foraging habitats,

allowing us to evaluate birds that used only one of the three focal habitat types.

For each breeding location, the percent of birds that wintered in aquaculture, natural freshwater, and marine habitats was calculated for males and females separately (Figure 4.2) and for both sexes combined (Figure 4.3). A χ^2 test was used to test variation in winter foraging habitat use across breeding locations and between males and females. A regression of percent habitat use by type (aquaculture, marine, freshwater), and breeding longitude (Figure 4.3), was used to describe regional trends in winter habitat use.

Results

Stable isotope values of feathers collected from wintering cormorants exhibited significant variation in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ ($p < 0.001$ for each) among foraging habitat types (aquaculture, natural freshwater, and marine; Table 4.1).

Table 4.1. Average ± SD of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values measured in feathers from Double-crested Cormorants (*Phalacrocorax auritus*) wintering in three different habitat types (aquaculture, natural freshwater, and marine) in the southeastern United States during 2011 and 2012. Values of each isotope differed significantly ($p < 0.001$) among habitat types.

Habitat type	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
Aquaculture	20	-20.2 ± 1.3	13.0 ± 0.9	0.5 ± 1.5
Freshwater	28	-27.0 ± 1.3	17.3 ± 0.9	3.4 ± 1.2
Marine	19	-19.9 ± 0.6	16.6 ± 0.4	13.2 ± 0.6

Based on their stable isotope values, nuptial plumes collected from breeding cormorants were classified into one of these three winter foraging habitat types using a discriminant analysis. Ten feather samples were eliminated from further analysis, as they did not meet the 95% exclusion threshold on the posterior probability of membership to one of these three habitat

types. The distribution of winter habitat type varied significantly across breeding colonies (χ^2=29.7; p<0.001) and between males and females (χ^2=20.1; p<0.001; Figure 4.2).

Figure 4.2. Winter habitat use (% of birds using natural freshwater, marine, or aquaculture) of male (N=66) and female (N=62) Double-crested Cormorants (*Phalacrocorax auritus*) breeding across eastern North America from 2010 to 2012.

More specifically, the percent of birds wintering in aquaculture habitats varied parabolically with breeding longitude (p<0.05, R^2=0.910; Figure 4.3), increasing from Minnesota

(11%) to the Great Lakes (with a peak in Lake Erie for pooled sexes [43%; Figure 4.3] and a peak in Lake Huron for males [86%; Figure 4.2]), then declining towards Lake Champlain (31%). Of birds that wintered in aquaculture habitats, 82% were found breeding in the Great Lakes (Lake Michigan, Lake Huron, and Lake Erie combined). From west to east, a pattern of increasing percent of marine habitat use (from 4% in Minnesota to 40% in Lake Champlain; $p<0.05$) and decreasing proportion of natural freshwater habitat use (from 85% in Minnesota to 29% in Lake Champlain; ns) was also observed (Figure 4.3).

The proportion of males to females differed significantly among winter habitat types ($\chi^2=20.1$; $p<0.001$). More males used aquaculture habitats (68% male; 32% female), more females used marine habitats (83% female; 17% male), and freshwater habitats were used relatively equally by both sexes (42% female; 58% male). Males and females also exhibited different patterns in winter habitat use across breeding locations (Figure 4.2).
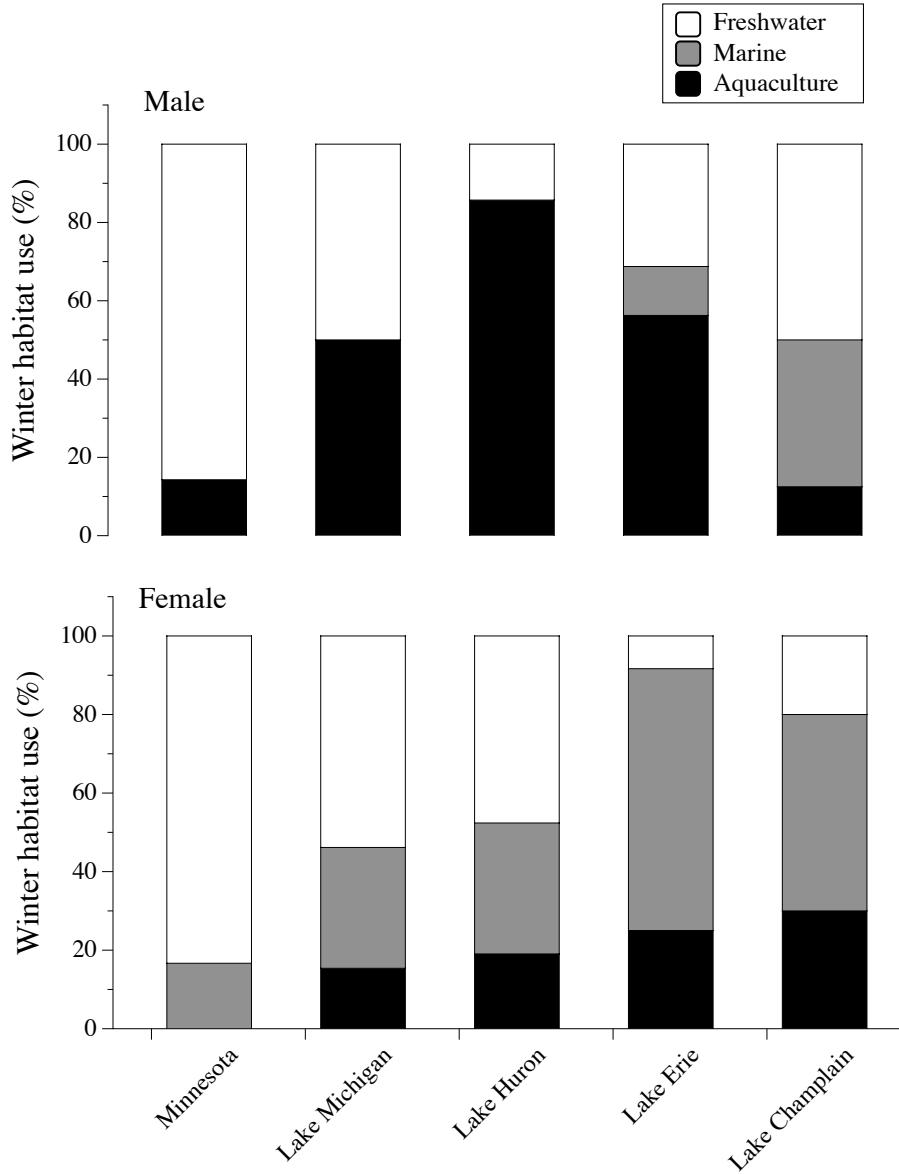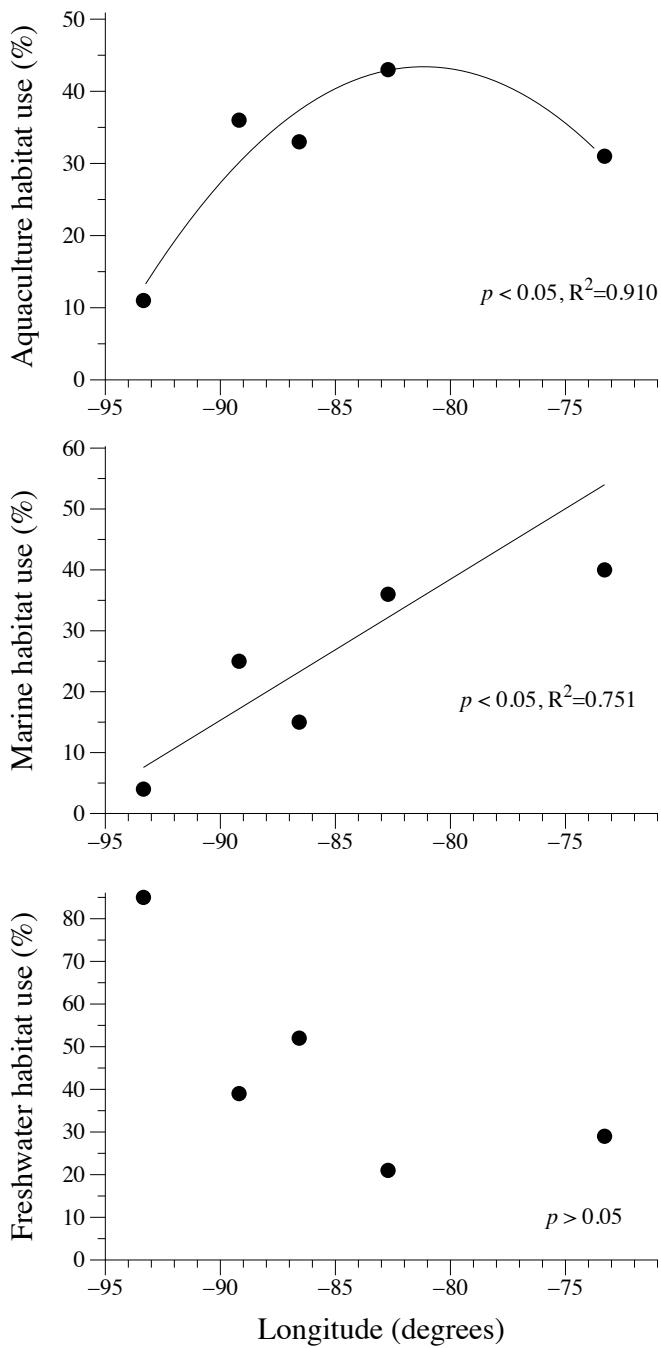
Figure 4.3. Winter habitat use (% of birds using natural freshwater, marine, or aquaculture) of Double-crested Cormorants (*Phalacrocorax auritus*) breeding across eastern North America from 2010 to 2012 (by longitude).

Discussion

This study is the first to provide dietary confirmation of winter resource use in Double-crested Cormorants breeding across eastern North America. Significant variation in winter habitat use was observed. As expected, birds in the Great Lakes (particularly Lake Huron and Lake Erie) had the greatest proportion of aquaculture resource use, but interestingly, some proportion of every breeding population wintered in aquaculture habitats. This suggests that cormorants foraging in aquaculture habitats are drawn from a broad breeding range (Dolbeer 1991, King et al. 2010). The observed distribution of birds wintering in aquaculture habitats supports the hypothesized division in cormorant migratory routes, with birds breeding in the western Great Lakes utilizing the Mississippi flyway and birds breeding in the eastern Great Lakes towards the Atlantic Coast utilizing the Atlantic flyway (Dolbeer 1991, King et al. 2010, Scherr et al. 2010, Guillaumet et al. 2011, King et al. 2012*a, b*, Chastant et al. 2013). From western to eastern breeding colonies, use of marine winter habitat increased, indicating that coastal environments may be the most critical foraging habitats for birds nesting in the eastern extent of the breeding range.

Males and females exhibited significant differences in winter habitat use, with a greater proportion of males foraging in aquaculture habitats and a greater proportion of females foraging in marine habitats. Sexual segregation in foraging behavior has been observed in other cormorant species (Van Eerden and Munsterman 1995, Bearhop et al. 2006, Quintana et al. 2010), although very few studies of wintering Double-crested Cormorant have detected it (Glahn et al. 1995). Males, which are the slightly larger sex, may potentially outcompete females for high prey-density aquaculture habitats, and may be better suited to manipulate spiny fish. Alternatively, females may preferentially forage in natural habitats for the greater quality and nutritional value

of prey (Nettleton and Exler 1992) and reduced exposure to management activities.

Management Implications

Studies have observed that cormorants wintering in aquaculture habitats primarily breed in the western Great Lakes (Dolbeer 1991, King et al. 2010, Guillaumet et al. 2011, King et al. 2012*b*), making these colonies potential targets for cormorant population management to mitigate aquaculture depredation. However, we observed that colonies across the entire eastern breeding range exhibited a substantial proportion of aquaculture resource use (Figure 4.3). For this reason, management of breeding birds in the Great Lakes alone may not alleviate aquaculture depredation, as birds breeding further west and east may increasingly contribute to the problem. Furthermore, when employed, the strategy of culling birds on the breeding grounds removes both males and females indiscriminately, and as a significantly greater proportion of males forage in aquaculture habitats than females, this strategy does not efficiently target the sex primarily responsible for aquaculture depredation. Together these observations suggest that targeting breeding birds is unlikely to be efficient in reducing aquaculture depredation by wintering cormorants. We therefore suggest that focusing management efforts at the site of depredation may prove to be a more efficient and effective strategy.

REFERENCES

Bearhop, S., D. Thompson, S. Waldron, I. Russell, G. Alexander, and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. Journal of Applied Ecology 36:75–84.

Bearhop, S., R. A. Phillips, R. McGill, Y. Cherel, D. A. Dawson, and J. P. Croxall. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Volume 311. Marine Ecology Progress Series.

Bond, A., and I. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. Marine Ornithology 37:183–188.

Chang, Y.-M., K. A. Hatch, T.-S. Ding, D. L. Eggett, H.-W. Yuan, and B. L. Roeder. 2008. Using stable isotopes to unravel and predict the origins of Great Cormorants (*Phalacrocorax carbo sinensis*) overwintering at Kinmen. Rapid Communications in Mass Spectrometry 22:1235–1244.

Chastant, J. E., D. T. King, D. V. C. Weseloh, and D. J. Moore. 2013. Population dynamics of Double-crested Cormorants in two interior breeding areas. The Journal of Wildlife Management 78:3–11.

Craig, E. C., S. B. Elbin, J. A. Danoff-Burg, and M. I. Palmer. 2012. Impacts of Double-crested Cormorants (*Phalacrocorax auritus*) and other colonial waterbirds on plant and arthropod communities on islands in an urban estuary. Waterbirds 35 (special publication 1):4–12.

Cuthbert, F. J., L. R. Wires, and J. McKearnan. 2002. Potential impacts of nesting Double-crested Cormorants on Great Blue Herons and Black-crowned Night-Herons in the US Great Lakes region. Journal of Great Lakes Research 28:145–154.

Diana, J. S., S. L. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. Journal of Great Lakes Research 32:306–320.

Dolbeer, R. 1991. Migration Patterns of Double-crested Cormorants East of the Rocky Mountains. Journal of Field Ornithology 62:83–93.

Dorr, B. S., L. W. Burger, S. C. Barras, and K. C. Godwin. 2012*a*. Economic impact of Double-

crested Cormorant, *Phalacrocorax auritus*, depredation on channel catfish, *Ictalurus punctatus*, aquaculture in Mississippi, USA. Journal of the World Aquaculture Society 43:502–513.

Dorr, B. S., S. L. Hanisch, P. H. Butchko, and D. G. Fielder. 2012*b*. Management of Double-crested Cormorants to improve sport fisheries in Michigan: three case studies. Human-Wildlife Interactions 6:155–168.

Doucette, J. L., B. Wissel, and C. M. Somers. 2011. Cormorant-fisheries conflicts: stable isotopes reveal a consistent niche for avian piscivores in diverse food webs. Ecological Applications 21:2987–3001.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40:503–537.

Glahn, J. F., and D. T. King. 2004. Bird depredation. Pages 1–27 *in* C. Tucker and J. Hargreaves, editors. Biology and culture of channel catfish. Elsiver, Amersterdam, The Netherlands.

Glahn, J. F., M. E. Tobin, and B. F. Blackwell. 2000*a*. A science-based initiative to manage Double-crested Cormorant damage to southern aquaculture. USDA National Wildlife Research Center - Staff Publications. Paper 532.

Glahn, J. F., M. E. Tobin, and J. B. Harrel. 1997. Possible effects of catfish exploitation on overwinter body condition of Double-crested Cormorants. Symposium on Double-crested Cormorants: population status and management issues in the Midwest Paper 11:107–113.

Glahn, J., and A. R. Stickley Jr. 1995. Wintering Double-crested Cormorants in the Delta region of Mississippi: population levels and their impact on the catfish industry. Colonial Waterbirds 18:137–142.

Glahn, J., and B. S. Dorr. 2002. Captive Double-crested Cormorant *Phalacrocorax auritus* predation on channel catfish *Ictalurus punctatus* fingerlings and its influence on single-batch cropping production. Journal of the World Aquaculture Society 33:85–93.

Glahn, J., and K. Brugger. 1995. The impact of Double-crested Cormorants on the Mississippi Delta catfish industry: A bioenergetics model. Colonial Waterbirds 18:168–175.

Glahn, J., D. Reinhold, and C. Sloan. 2000*b*. Recent population trends of Double-crested

Cormorants wintering in the Delta region of Mississippi: responses to roost dispersal and removal under a recent depredation order. Waterbirds 23:38–44.

Glahn, J., P. Dixson, G. Littauer, and R. McCoy. 1995. Food habits of Double-crested Cormorants wintering in the Delta region of Mississippi. Colonial Waterbirds 18:158–167.

Glahn, J., S. J. Werner, T. Hanson, and C. Engle. 2002. Cormorant depredation losses and their prevention at catfish farms: economic considerations. Human Conflicts with Wildlife: Economic Considerations Paper 17:138–146.

Guillaumet, A., B. Dorr, G. Wang, J. D. Taylor, R. B. Chipman, H. Scherr, J. Bowman, K. F. Abraham, T. J. Doyle, and E. Cranker. 2011. Determinants of local and migratory movements of Great Lakes Double-crested Cormorants. Behavioral Ecology 22:1096–1103.

Hatch, J. J. 1995. Changing populations of Double-crested Cormorants. Colonial Waterbirds 18:8–24.

Hatch, J. J. and D. V. C. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). No. 441 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hebert, C. E., D. V. C. Weseloh, A. Idrissi, M. T. Arts, and E. Roseman. 2009. Diets of aquatic birds reflect changes in the Lake Huron ecosystem. Aquatic Ecosystem Health & Management 12:37–44.

Hebert, C. E., J. Duffe, D. V. C. Weseloh, E. Senese, and G. Haffner. 2005. Unique island habitats may be threatened by Double-crested Cormorants. Journal of Wildlife Management 69:68–76.

Hebert, C. E., M. Bur, D. Sherman, and J. L. Shutt. 2008. Sulfur isotopes link overwinter habitat use and breeding condition in Double-crested Cormorants. Ecological Applications 18:561–567.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326.

Hobson, K. A. 2009. Trophic interactions between cormorants and fisheries: towards a more

quantitative approach using stable isotopes. Waterbirds 32:481–490.

Hobson, K. A., and R. G. Clark. 1992*a*. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94:181–188.

Hobson, K. A., and R. G. Clark. 1992*b*. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189–197.

Hobson, K. A., K. Hughes, and P. Ewins. 1997. Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. Auk 114:467–478.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

King, D. T., B. Blackwell, B. Dorr, and J. L. Belant. 2010. Effects of aquaculture on migration and movement patterns of Double-crested Cormorants. Human-Wildlife Conflicts 4:77–86.

King, D. T., B. K. Strickland, and A. A. Radomski. 2012*a*. Winter and summer home ranges and core use areas of Double-crested Cormorants captured near aquaculture facilities in the southeastern United States. Waterbirds 35:124–131. BioOne.

King, D. T., B. K. Strickland, and A. Radomski. 2012*b*. Migration patterns of Double-crested Cormorants wintering in the southeastern United States. Waterbirds 35:132–137.

King, D., J. Glahn, and K. Andrews. 1995. Daily activity budgets and movements of winter roosting Double-crested Cormorants determined by biotelemetry in the Delta region of Mississippi. Colonial Waterbirds 18:152–157.

Kolb, G. S., L. Jerling, C. Essenberg, C. Palmborg, and P. A. Hambäck. 2012. The impact of nesting cormorants on plant and arthropod diversity. Ecography 35:726–740.

Lott, C. A., T. Meehan, and J. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. Oecologia 134:505–510.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further

evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Mizutani, H., M. Fukuda, Y. Kabaya, and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk 107:400–403.

Nettleton, J. A., and J. Exler. 1992. Nutrients in wild and farmed fish and shellfish. Journal of Food Science 57:257–260.

Neuman, J., D. Pearl, P. Ewins, R. Black, D. V. C. Weseloh, M. Pike, and K. Karwowski. 1997. Spatial and temporal variation in the diet of double-crested cormorants (Phalacrocorax auritus) breeding on the lower Great Lakes in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 54:1569–1584.

Ofukany, A., K. Hobson, and L. I. Wassenaar. 2012. Connecting breeding and wintering habitats of migratory piscivorous birds: implications for tracking contaminants (Hg) using multiple stable isotopes. Environmental Science & Technology 46:3253–3262.

Oppel, S., and A. N. Powell. 2008. Assigning King Eiders to wintering regions in the Bering Sea using stable isotopes of feathers and claws. Marine Ecology Progress Series 373:149–156.

Quintana, F., R. Wilson, P. DellArciprete, E. Shepard, and A. G. Laich. 2010. Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant *Phalacrocorax atriceps* a colonial seabird. Oikos 120:350–358.

Ridgway, M. S., J. B. Pollard, and D. V. C. Weseloh. 2006. Density-dependent growth of Double-crested Cormorant colonies on Lake Huron. Canadian Journal Of Zoology-Revue Canadienne De Zoologie 84:1409–1420.

Rudstam, L., A. VanDeValk, C. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14:149–163.

SAS Institute. 2013. JMP statistical discovery software. Eleventh edition. SAS institute, Cary, NC.

Scherr, H., J. Bowman, and K. F. Abraham. 2010. Migration and winter movements of Double-crested Cormorants breeding in Georgian Bay, Ontario. Waterbirds 33:451–460.

Somers, C. M., J. L. Doucette, D. V. C. Weseloh, V. A. Kjoss, and R. M. Brigham. 2011. Interactions between Double-crested Cormorants and other ground-nesting species. Waterbirds 34:168–176.

Somers, C. M., M. N. Lozer, and J. S. Quinn. 2007. Interactions between Double-crested Cormorants and Herring Gulls at a shared breeding site. Waterbirds 30:241–250.

Steele, K. W., and R. M. Daniel. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. Journal of Agricultural Science 90:7–9.

Taylor, J., and B. S. Dorr. 2003. Double-crested Cormorant impacts to commercial and natural resources. Wildlife Damage Management Conference 10:43–51.

Tobin, M. E., D. T. King, B. S. Dorr, S. J. Werner, and D. S. Reinhold. 2002. Effect of roost harassment on cormorant movements and roosting in the delta region of Mississippi. Waterbirds 25:44–51.

Van Eerden, M. R., and M. Munsterman. 1995. Sex and age-dependent distribution in wintering cormorants *Phalacrocorax carbo sinensis* in western Europe. Ardea 83:285–297.

Weseloh, D. V. C., C. Pekarik, T. Havelka, G. Barrett, and J. Reid. 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. Journal of Great Lakes Research 28:125–144.

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the Double-crested Cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. Waterbirds 29:9–37.

CHAPTER 5

SEASONAL INTERACTIONS PLAY A LIMITED ROLE IN DOUBLE-CRESTED
CORMORANT (*PHALACROCORAX AURITUS*) LIFE HISTORY

Elizabeth Craig[1], Tommy King[2], Jed Sparks[3], Paul Curtis[4]

[1] Field of Zoology and Wildlife Conservation,
Cornell University, Ithaca, NY, 14853, USA

[2] United States Department of Agriculture, Wildlife Services, National Wildlife Research Center,
Mississippi Field Station, Mississippi State, MS 39762, USA

[3] Department of Ecology and Evolutionary Biology,
Cornell University, Ithaca, NY, 14853, USA

[4] Department of Natural Resources,
Cornell University, Ithaca, NY, 14853, USA

Abstract

Seasonal interactions occur when events in one season produce carry-over effects on an individual in a subsequent season. We evaluated the importance of seasonal interactions in the life history of a migratory waterbird, the Double-crested Cormorant (*Phalacrocorax auritus*), by observing the effect of winter foraging decisions (the use of aquaculture, natural freshwater, or marine habitat types) on body condition and reproductive output during the subsequent breeding season. We hypothesized that use of aquaculture habitat would result in a positive seasonal interaction because cormorants wintering at aquaculture facilities exhibited better body condition than those wintering in natural freshwater environments, likely due to high fish-stocking densities in aquaculture ponds. In May 2013, breeding birds were captured at their nesting colonies in Lake Champlain, New York. Winter-grown feathers were sampled for stable isotope analysis to determine foraging habitat type. Body condition and reproductive output were recorded during capture activities. We found that reproductive output correlated positively with body condition ($p<0.05$), confirming that our metrics were biologically meaningful. However, counter to our prediction, cormorants wintering in aquaculture habitats did not exhibit better body condition or reproductive output than birds wintering in natural freshwater and marine habitats. Overall, we found no evidence of significant seasonal interactions in this system. We concluded that wintering in aquaculture habitats yields no more than ephemeral benefits for cormorants. While the use of aquaculture resources may influence cormorant population dynamics through improved body condition and subsequent increases in winter survival rates, there is no evidence that it affects reproductive rates in this species.

Introduction

Seasonal interactions, the phenomenon in which events occurring in one season produce carry-over effects on an individual in a subsequent season, play a role in the life histories of many species. They are particularly important when their influence on the condition or reproduction of an individual is large. Migratory birds provide some of the most interesting and complex examples of this phenomenon, as these animals experience drastic changes in environmental conditions across seasons. Seasonal interactions have been documented in groups such as migratory songbirds, waterfowl, shorebirds, and waterbirds (Gunnarsson et al. 2005, Hebert et al. 2008, Reudink et al. 2009*a*, *b*, Inger et al. 2010). Technologies, both new and improved, have created novel opportunities to observe the behavior and condition of animals over an extended spatial and temporal range (Webster *et al*. 2002). In response, the literature concerning interactions between non-breeding and breeding season events has expanded in recent years, providing overwhelming support for the biological significance of seasonal interactions (see reviews in Webster et al. 2002, Drent et al. 2006, Norris and Marra 2007). However, this field is still in its infancy, and studies have only recently begun to make conclusive links between non-breeding season events and reproductive success (e.g. Norris et al. 2004, Gunnarsson et al. 2005, Reudink et al. 2009b, Inger et al. 2010).

We evaluated the importance of seasonal interactions in the life history of a migratory waterbird, the Double-crested Cormorant (*Phalacrocorax auritus*), by observing the effect of winter foraging decisions (the use of aquaculture, natural freshwater, or marine habitat types) on body condition and reproductive output during the subsequent breeding season. The cormorant family (Phalacrocoracidae) has a worldwide distribution (Johnsgard 1993) and in many instances, is subject to intense study and management due to conflicts with fisheries. Despite

considerable interest in cormorant foraging ecology and population dynamics, few studies have considered the effects of winter events on cormorant condition (Glahn et al. 1997, Hebert et al. 2008, Scherr et al. 2010), and none have investigated the implications for reproductive success. Our study is the first to investigate the seasonal interactions of winter events on individual fitness in this ubiquitous and controversial family.

The Double-crested Cormorant is a fish-eating, aquatic predator native to North America. Populations of cormorants breeding in eastern North America tend to overwinter along Atlantic and Gulf coasts, and at inland lakes, rivers and ponds in the southeastern United States (Hatch and Weseloh 1999, King et al. 2010, Scherr et al. 2010). This species exhibits very little migratory connectivity, such that individuals from a single colony tend to overwinter in a range of aquatic environments including aquaculture, marine, and natural freshwater habitats (Scherr et al. 2010, Guillaumet et al. 2011). Researchers have hypothesized that foraging in aquaculture habitats might result in a positive seasonal interaction because cormorants wintering at aquaculture facilities have exhibited better body condition than those wintering in natural freshwater environments, likely due to high fish-stocking densities in aquaculture ponds (Glahn et al. 1997, Hebert et al. 2008). Cormorants foraging in freshwater environments (both natural and aquaculture) have also exhibited better body condition than those foraging in marine environments (Hebert et al. 2008) potentially due to the physiological costs of salt excretion (Norris 2006), or higher energetic foraging costs.

We tested this hypothesis through two objectives: 1) to determine whether winter foraging decisions influenced summer body condition of cormorants across the breeding range in the eastern United States, and 2) to observe whether winter foraging decisions influenced reproductive output of cormorants at a single breeding location. Evaluating the importance of

seasonal interactions in this species will elucidate the mechanisms by which human land-use change, in this case increasing intensive aquaculture in the southeastern United States, influence wildlife populations.

Methods

To address our first objective, cormorants culled during management activities were collected from breeding colonies at Wells Lake (44.291 N, -93.342 W) in southern Minnesota (*n*=30), Garden Bay (45.780 N, -86.577 W) in northern Lake Michigan, Michigan (*n*=28), Thunder Bay (44.999 N, -83.361 W) in western Lake Huron, Michigan (*n*=30), Turning Point Island (41.457 N, -82.727 W) in southwest Lake Erie, Ohio (*n*=30), and Young Island (44.740 N, -73.345 W) in Lake Champlain, Vermont (*n*=20) during April and May of 2010 and 2012. These locations were chosen to span the cormorant breeding range in eastern North America, and because each had active cormorant management programs from which culled birds could be collected. Breeding locations were limited to the United States for permitting reasons. At least two nuptial plumes were collected from each bird and stored in envelopes for stable isotope analysis. The sex of each bird was determined by dissection. Morphological measurements were taken from each bird including weight, culmen length and depth, tarsus length, flat wing length, and total length from tip of bill to tip of tail. These measurements were used to determine body condition. A principal component analysis was conducted using all of the morphological measurements except weight. Principal Component 1, representing overall body size, was regressed against weight. The residual weight of each bird (the amount by which a bird was above or below average weight based on its size) was recorded and used as an indicator of relative body condition as per Hebert *et al.* (2008).

To address our second objective, we observed reproductive output of live adult cormorants breeding at colonies on the Four Brothers Islands (44.428 N, -73.332 W) located in Lake Champlain, New York during May 2013. This site was chosen because cormorants breeding on Lake Champlain had been observed to winter in relatively equal proportions at aquaculture, natural freshwater, and marine habitats (Chapter 4), improving the probability of attaining equal sample sizes of birds from each of these winter habitat types. We labeled and monitored 170 cormorant nests. It was not possible to observe the fledge rate of these nests, as many eggs had been oiled for population management. Therefore the length and width of every egg in each nest were measured and used to calculate egg volume (Coulson et al. 1969), a parameter which correlates with the survival, body mass, and growth of waterbird chicks (Parsons 1970, Stokland and Amundsen 1988, Amundsen and Stokland 1990). Clutch volume (the sum of the volume for all eggs in the nest), and average egg volume (the average volume for all eggs in the nest), were calculated and used as indicators of reproductive output.

Adult cormorants were successfully trapped at 73 nests using modified padded foot-hold traps (King *et al*. 1998). Morphological measurements were taken from each bird as in objective one. These measurements were used as indicators of body condition, as described above, and to classify sex. Body condition was therefore measured twice on Lake Champlain. Sexes are difficult to distinguish visually, but males are slightly larger than females, and sex can be identified using a discriminant model (Glahn and McCoy 1995). The morphological data were entered into a discriminant model informed by data collected from known-sex birds culled at Lake Champlain in 2010 (Chapter 4) yielding 95% accuracy in sex identification. Of the 73 adults successfully trapped, only 36 still displayed nuptial plumes. At least two feathers were collected from each bird for stable isotope analysis.

Stable isotope analysis

We exploited the natural variation in stable isotope values that exists among three habitat types (aquaculture, natural freshwater, and marine), allowing for the remote identification of winter foraging habitats used by cormorants. We confirmed in Chapter 4 that cormorants wintering in each of these aquatic habitat types could be distinguished using stable isotope values of carbon (δ^{13}C), nitrogen (δ^{15}N) and sulfur (δ^{34}S). Because stable isotope values in feathers represent the diet of the animal at the time of feather formation (Hobson and Clark 1992, Bearhop et al. 2003, 2004, Oppel and Powell 2008, Hobson 2009), feathers grown during the winter contain information about winter resource use. We used nuptial plumes as an indicator of winter resource use, as these feathers are grown in late winter and then displayed during courtship on the breeding grounds.

One feather from each bird was analyzed for δ^{13}C and δ^{15}N. A 1-mg sample (± 0.1 mg) of each feather was encapsulated in tin and analyzed for δ^{13}C and δ^{15}N using a Thermo Finnigan Delta V Advantage isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyzer (EA) at Cornell University's Stable Isotope Laboratory. An internal laboratory standard of mink (*Neovison vison*) tissue was analyzed for every ten unknowns. A chemical methionine standard was used to measure instrumental accuracy across a gradient of amplitude intensities. Isotope corrections were performed using a two-point normalization (linear regression) of all raw δ^{13}C and δ^{15}N data with two additional in-house standards: Cayuga Lake brown trout (*Salmo trutta*) and corn (*Zea mays*). Based on standard deviations from within-run replicate measurements of standards, analytical error was estimated to be $\pm 0.2‰$ for δ^{13}C, and $\pm 0.3‰$ for δ^{15}N. A second feather from each bird was analyzed for δ^{34}S. A 1-mg sample (± 0.1 mg) of each feather was encapsulated in tin and analyzed for δ^{34}S at the University of Utah's Stable Isotope

Ratio Facility for Environmental Research using EA-IRMS. Internal laboratory standards were analyzed for every ten unknowns. Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be $\pm 0.3‰$ for $\delta^{34}S$.

Statistical analysis

All statistical analyses were conducted using JMP statistical software (SAS Institute 2013). Isotope data from nuptial plumes were entered into the discriminant model developed in Chapter 4 to determine the foraging habitat type cormorants predominantly used during the previous winter. An exclusion threshold of 95% was applied to the posterior probability of membership (Oppel and Powell 2008) to remove individuals from the analysis that used a mix of winter foraging habitats ($n=4$), allowing us to evaluate birds that used only one of the three focal habitat types ($n=32$). To determine whether winter habitat type influenced breeding season condition and reproductive success, analysis of variances (ANOVA; with Tukey-Kramer HSD) of the body condition and reproductive output data were conducted using winter habitat type as the factor.

To confirm that average egg volume and clutch volume were biologically meaningful measurements, we tested the assumption that meaningful reproductive parameters should correlate positively with summer body condition. Females in better body condition should produce higher reproductive output, and higher quality males, which arrive first on the breeding grounds to establish nesting territories, should attract higher quality females (Johnsgard 1993, Glahn et al. 1997). This general assumption was confirmed, as regressions of average egg volume and clutch volume against body condition revealed significant positive correlations ($p<0.05$ for both; Figure 5.1).
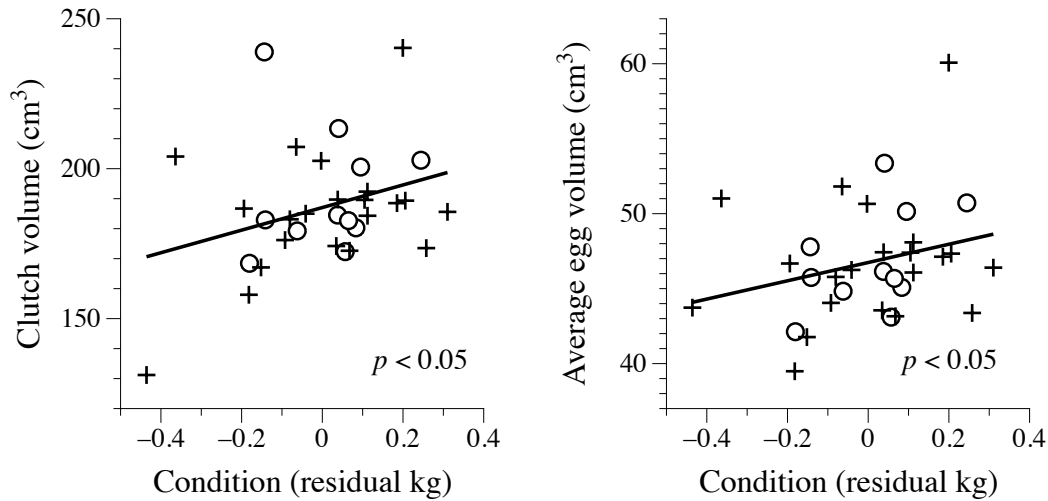
Figure 5.1. Linear regression of reproductive output (average egg volume and clutch volume) against body condition (residuals from regression of weight against body size) of male (+) and female (O) Double-crested Cormorants (*Phalacrocorax auritus*) breeding on Lake Champlain, New York, in 2013.

Results

Objective 1

Summer body condition (residual weight) had a mean of 0.00 kg at all breeding locations and ranged from -0.18 to 0.15 kg in Minnesota, -0.30 to 0.22 kg at Lake Michigan, -0.21 to 0.26 kg at Lake Huron, -0.25 to 0.25 kg at Lake Erie, and -0.38 to 0.31 kg at Lake Champlain. Based on ANOVA with Tukey-Kramer HSD, a significant effect of winter habitat on summer body condition was observed at Lake Champlain during 2010 ($p < 0.05$), where cormorants wintering in marine habitats exhibited worse summer body condition than birds from aquaculture or natural freshwater habitats. However, no effect was observed when body condition measurements were repeated at Lake Champlain in 2013, nor was an effect observed at any other breeding location (Table 5.1).

Table 5.1. Average body condition measurements (residual kg) for Double-crested Cormorants (*Phalacrocorax auritus*) breeding at five locations (Minnesota, Lake Michigan, Lake Huron, Lake Erie, and Lake Champlain) across the eastern United States based on type of foraging habitat (aquaculture, natural freshwater, and marine) used during the previous winter. Different superscript letters represent significant differences in body condition among habitat type according to Tukey-Kramer HSD (n.s.: not significant).

| Breeding location | Year | n | Mean condition (residual kg) ± SE | | | *p*-value |
			Aquaculture	Freshwater	Marine	
Minnesota	2012	30	-0.02 ± 0.06	0.00 ± 0.02	0.00 ± 0.10	n.s.
Lake Michigan	2012	28	0.01 ± 0.05	-0.05 ± 0.04	0.10 ± 0.08	n.s.
Lake Huron	2012	30	0.01 ± 0.03	-0.03 ± 0.02	0.01 ± 0.03	n.s.
Lake Erie	2010	30	-0.03 ± 0.04	0.05 ± 0.05	0.01 ± 0.04	n.s.
Lake Champlain	2010	20	0.14 ± 0.08[a]	0.13 ± 0.07[a]	-0.10 ± 0.06[b]	*p* < 0.05
Lake Champlain	2013	32	-0.01 ± 0.06	0.03 ± 0.05	-0.03 ± 0.05	n.s.

Objective 2

From the 170 nests monitored on Lake Champlain, clutch volume exhibited a mean (± SE) of 184.9 ± 1.8 cm^3 and ranged from 122.4 to 298.0 cm^3 while average egg volume exhibited a mean (± SE) of 47.3 ± 0.3 cm^3 and ranged from 39.5 to 74.5 cm^3. Of the 32 adults from which feathers were collected, 66% were male (*n*=21) and 34% were female (*n*=11). Winter habitat use was distributed with 28% in aquaculture (*n*=8), 33% in natural freshwater (*n*=11), and 39% in marine habitats (*n*=13). ANOVA revealed no significant effect of winter habitat type on clutch volume (*p*=0.96), or average egg volume (*p*=0.92; Table 5.2).

83

Table 5.2. Reproductive output (mean ± SE for clutch size, clutch volume, and average egg volume) for Double-crested Cormorants (*Phalacrocorax auritus*) breeding at Lake Champlain, New York, in 2013 (n=170) based on foraging habitat type (aquaculture, natural freshwater, and marine) used during the previous winter.

Reproductive output	Aquaculture	Freshwater	Marine
Clutch size (# eggs)	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.1
Clutch volume (cm^3)	185.8 ± 7.6	188.8 ± 6.5	187.2 ± 5.9
Average egg volume (cm^3)	46.4 ± 1.4	47.2 ± 1.2	46.7 ± 1.1

Discussion

Our hypothesis that cormorants wintering in aquaculture habitats would experience a positive seasonal interaction was not supported by the data. Only at Lake Champlain during 2010 did we observe breeding cormorants with better body condition if they wintered in aquaculture or natural freshwater habitats rather than in marine environments. This effect was not observed at Lake Champlain in 2013. Furthermore, no seasonal interaction, either positive or negative, was observed between winter foraging habitat and summer body condition at any other breeding colony across the range (Table 5.1). Counter to our prediction, cormorants wintering in aquaculture habitats did not exhibit higher reproductive output than birds wintering in natural freshwater or marine habitats. While small sample sizes may influence the lack of statistical significance, the body condition and reproductive data exhibited no trends among winter habitat types whatsoever, suggesting that the results might not differ even if this study were to be repeated with much larger sample sizes. Overall, we found no evidence of a significant carry-over effect associated with winter habitat type.

Despite observations of improved body condition for birds wintering in aquaculture habitats (Glahn et al. 1997), these benefits may be rendered ephemeral by the significant trade-

offs of wintering in anthropogenic environments. Cormorants are heavily managed in aquaculture habitats (Glahn et al. 2000), and management activities (including harassment and culling of cormorants at aquaculture ponds and nighttime roosts) may create a stressful environment for wintering birds. In addition, farmed fish may not provide the same nutritional value as wild fish (Nettleton and Exler 1992). Finally, birds wintering in aquaculture habitats, which are centered in the delta region of Mississippi in the Mississippi Flyway (Dorr et al. 2008, King et al. 2012*a, b*), may experience greater migration distances to the Lake Champlain breeding colony than birds wintering in natural freshwater and marine environments, which are prevalent along the Atlantic Flyway.

Human land-use change, in this case intensive aquaculture development in the southeastern United States, has influenced cormorant populations by attracting large numbers of birds to densely-stocked fish ponds (Glahn and King 2004, Dorr et al. 2008). However, foraging in these attractive aquaculture habitats comes at the cost of increased harassment, and may provide only ephemeral benefits to the individual, as any relative improvements in body condition are lost by the time birds arrive on the breeding grounds (Table 5.1). Aquaculture may influence cormorant population dynamics through improved body condition and subsequent increases in survival rates over the winter (Glahn et al. 1997, Blackwell et al. 2002), but we found no evidence that aquaculture resource use influences reproductive rates in Double-crested Cormorants.

REFERENCES

Amundsen, T., and J. Stokland. 1990. Egg size and parental quality influence nestling growth in the Shag. Auk 107:410–413.

Bearhop, S., G. Hilton, S. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society of London Series B-Biological Sciences 271:S215–S218.

Bearhop, S., R. W. Furness, G. Hilton, S. Votier, and S. Waldron. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. Functional Ecology 17:270–275.

Blackwell, B. F., M. A. Stapanian, and D. C. Weseloh. 2002. Dynamics of the Double-crested Cormorant population on Lake Ontario. Wildlife Society Bulletin:345–353.

Coulson, J., G. Potts, and J. Horobin. 1969. Variation in eggs of shag (*Phalacrocorax aristotelis*). Auk 86:232–&.

Dorr, B. S., L. W. Burger, and S. C. Barras. 2008. Evaluation of aerial cluster sampling of Double-crested Cormorants on aquaculture ponds in Mississippi. Journal of Wildlife Management 72:1634–1640.

Drent, R., A. D. Fox, and J. Stahl. 2006. Travelling to breed. Journal of Ornithology 147:122–134.

Glahn, J. F., and D. T. King. 2004. Bird depredation. Pages 1–27 *in* C. Tucker and J. Hargreaves, editors. Biology and culture of channel catfish. Elsiver, Amersterdam, The Netherlands.

Glahn, J. F., M. E. Tobin, and B. F. Blackwell. 2000. A science-based initiative to manage Double-crested Cormorant damage to southern aquaculture. USDA National Wildlife Research Center - Staff Publications. Paper 532.

Glahn, J. F., M. E. Tobin, and J. B. Harrel. 1997. Possible effects of catfish exploitation on overwinter body condition of Double-crested Cormorants. Symposium on Double-crested Cormorants: population status and management issues in the Midwest Paper 11:107–113.

Glahn, J., and R. McCoy. 1995. Measurements of wintering Double-crested Cormorants and discriminant models of sex. Journal of Field Ornithology 66:299–304.

Guillaumet, A., B. Dorr, G. Wang, J. D. Taylor, R. B. Chipman, H. Scherr, J. Bowman, K. F. Abraham, T. J. Doyle, and E. Cranker. 2011. Determinants of local and migratory movements of Great Lakes Double-crested Cormorants. Behavioral Ecology 22:1096–1103.

Gunnarsson, T., J. Gill, J. Newton, P. Potts, and W. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. Proceedings of the Royal Society B-Biological Sciences 272:2319.

Hatch, J. J. and D. V. C. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). No. 441 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hebert, C. E., M. Bur, D. Sherman, and J. L. Shutt. 2008. Sulfur isotopes link overwinter habitat use and breeding condition in Double-crested Cormorants. Ecological Applications 18:561–567.

Hobson, K. A. 2009. Trophic interactions between cormorants and fisheries: towards a more quantitative approach using stable isotopes. Waterbirds 32:481–490.

Hobson, K. A., and R. G. Clark. 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189–197.

Inger, R., X. Harrison, G. Ruxton, J. Newton, K. Colhoun, G. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. Journal of Animal Ecology 79:974–982.

Johnsgard, P. 1993. Cormorants, darters, and pelicans of the world. Smithsonian Institution Press, Washington.

King, D. T., B. Blackwell, B. Dorr, and J. L. Belant. 2010. Effects of aquaculture on migration and movement patterns of Double-crested Cormorants. Human-Wildlife Conflicts 4:77–86.

King, D. T., B. K. Strickland, and A. A. Radomski. 2012*a*. Winter and summer home ranges and

core use areas of Double-crested Cormorants captured near aquaculture facilities in the southeastern United States. Waterbirds 35:124–131.

King, D. T., B. K. Strickland, and A. Radomski. 2012*b*. Migration patterns of Double-crested Cormorants wintering in the southeastern United States. Waterbirds 35:132–137.

King, D., J. Paulson, D. Leblanc, and K. Bruce. 1998. Two capture techniques for American White Pelicans and Great Blue Herons. Colonial Waterbirds 21:258–260.

Nettleton, J. A., and J. Exler. 1992. Nutrients in wild and farmed fish and shellfish. Journal of Food Science 57:257–260.

Norris, D. 2006. Vertebrate Endocrinology. Pages 313–314. Fourth edition. Elsevier Academic Press.

Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. Condor 109:535–547.

Norris, D. R., P. P. Marra, R. Montgomerie, T. K. Kyser, and L. Ratcliffe. 2004. Reproductive effort, molting latitude, and feather color in a migratory songbird. Science 306:2249.

Oppel, S., and A. N. Powell. 2008. Assigning King Eiders to wintering regions in the Bering Sea using stable isotopes of feathers and claws. Marine Ecology Progress Series 373:149–156.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in Herring Gulls (*Larus argentatus*). Nature 228:1221–1222.

Reudink, M. W., C. E. Studds, P. P. Marra, T. K. Kyser, and L. M. Ratcliffe. 2009a. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American Redstart *Setophaga ruticilla*. Journal of Avian Biology 40:34–41.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009b. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society B-Biological Sciences 276:1619–1626.

SAS Institute. 2013. JMP statistical discovery software. Eleventh edition. SAS institute, Cary, NC.

Scherr, H., J. Bowman, and K. F. Abraham. 2010. Migration and winter movements of Double-crested Cormorants breeding in Georgian Bay, Ontario. Waterbirds 33:451–460.

Stokland, J., and T. Amundsen. 1988. Initial size hierarchy in broods of the shag - relative significance of egg size and hatching asynchrony. Auk 105:308–315.

Webster, M., P. P. Marra, S. Haig, S. Bensch, and R. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

CHAPTER 6

CONCLUSION

Summary of findings

My dissertation was unified by the use of stable isotope techniques to explore colonial

waterbird foraging ecology, and the application of findings to wildlife conservation and

management.

My first research chapter, Chapter 2 of this dissertation, used stable isotope analysis of

nestling waterbird feathers to identify the key foraging resources that support waterbird

populations during the critical stage of chick rearing. My approach yielded novel observations of

resource use in some species, particularly the Glossy Ibis (*Plegadis falcinellus*) and the Great

Black-backed Gull (*Larus marinus*), and confirmed previous assumptions about resource use in

others. I suggest that stable isotope results will serve as an excellent means to prioritize aquatic

habitats for protection and restoration based on their relative importance for waterbirds. These

results can also be used to modify and focus monitoring efforts on habitat types known to be of

particular importance to a focal population. An integrative approach of observational methods

and stable isotope analysis will therefore facilitate both the identification of a suite of potential

foraging sites, and the prioritization of those sites for waterbird conservation.

Chapter 3 of this dissertation presented the results of a collaborative captive feeding

study of Double-crested Cormorants (*Phalacrocorax auritus*) with scientists from the United

States Department of Agriculture, Animal and Plant Health Inspection Service-Wildlife Services,

and constitutes the jumping-off point in my research of this controversial species. The diet-tissue

discrimination factors measured in this study will be a valuable contribution to the future of

cormorant research.

The remainder of this dissertation focused on a major issue of human-wildlife conflict: the depredation of farmed fish, primarily channel catfish (*Ictalurus punctatus*), from aquaculture producers in the southeastern United States. Many scientists have explored this topic with the aim of documenting, understanding, and reducing the effects of cormorants on aquaculture in this region (reviewed in Chapters 4 and 5). My contribution to this field was in providing novel approaches for identifying birds involved in depredation remotely and noninvasively (Chapter 4) and, as opposed to observing the effects of cormorants on aquaculture, considering the reciprocal effect of aquaculture on the birds (Chapter 5).

My findings in Chapter 4 supported much of the research that has been accomplished to date concerning cormorant migration from wintering to breeding grounds. As expected, breeding colonies in the Great Lakes (particularly Lake Huron and Lake Erie) contained the greatest proportion of birds that had consumed aquaculture resources during the previous winter. Interestingly, however, some proportion of every breeding population wintered in aquaculture habitats. This led me to conclude that management of breeding birds in the Great Lakes may not alleviate aquaculture depredation, as birds breeding further west and east may increasingly contribute to the problem. The benefit of my stable isotope approach was to confirm cormorant depredation of aquaculture resources using dietary (i.e., stable isotope) information rather than assuming that birds contributed to depredation based on telemetry and band returns. My research presented a cost-effective and non-invasive method for identifying cormorant resource use over extended spatial and temporal scales.

My final research chapter, Chapter 5, evaluated the importance of seasonal interactions in the life history of Double-crested Cormorants; specifically the strength of the carry-over effect of

winter foraging behavior on summer body condition and reproductive output. I found little support for a carry-over effect on body condition at colonies across the breeding range in the eastern United States. Further investigations on Lake Champlain revealed no support for a carry-over effect on reproductive output. Overall, counter to my expectations and those expressed in the literature, my results led me to conclude that seasonal interactions of this type do not play a significant role in the life history of cormorants. Instead, breeding season events, such as the availability of fish and the foraging efficiency of the individual, may have the greatest influence on reproductive output, which is supported by the fact that cormorants, as income breeders, use exogenous resources for egg formation. However, if non-breeding season events that were not addressed in my research (e.g., winter foraging efficiency, migration distance, etc.) were to influence summer body condition of cormorants, such seasonal interactions could be significant, as evidenced by the correlation between summer body condition and reproductive output of cormorants on Lake Champlain (Chapter 5). It would be worthwhile, therefore, to further investigate the factors, both on and off the breeding grounds, that contribute to summer body condition in cormorants.

Final thoughts

My hypothesis, that birds wintering in aquaculture environments would have better body condition and reproductive output than birds wintering in natural environments, was based on the assumption that aquaculture resources provide a benefit to the individual, likely through increased foraging efficiency in densely-stocked fish ponds. In reality, the situation is likely far more complicated. I suggest that there are substantial trade-offs to foraging in anthropogenic environments, particularly in the case of fish farms, where farmers are permitted to harass and

lethally remove cormorants from their facilities. The stress of active management may counteract any physiological benefits that cormorants gain from higher food intake. However, aquaculture ponds are still highly attractive to cormorants, and birds that winter in aquaculture environments do not appear to have worse condition or reproductive output than those from natural environments. This suggests that the large potential costs and benefits of foraging in an anthropogenic environment may produce a similar effect on condition as the lower costs and benefits of foraging in natural environments, and that while the specific trade-offs differ, the end result in terms of fitness benefits may not. This would be an interesting area of inquiry, and I suggest that the examination of stress hormones, such as corticosterone deposited in feathers at the time of their formation, might shed light on the trade-offs involved in foraging in anthropogenic versus natural environments.

Management implications

My research has demonstrated the value of applying stable isotope techniques to a range of wildlife conservation and management issues. I recommend that stable isotope analysis be employed as a non-invasive, and relatively cost-effective method of monitoring resource use in wildlife populations of interest. Specifically, I suggest that my approach to monitoring foraging behavior of waterbirds in New York Harbor could be applied to good effect in prioritizing aquatic habitats for protection and restoration for other taxa and in other estuaries. Also, agencies monitoring and managing cormorants should continue to find a stable isotope approach to be of great value in remotely identifying resource use in this species. While my research focused on the breeding distribution of birds responsible for aquaculture depredation, my approach could be applied to birds on the wintering grounds (e.g., to determine which night roosts contain birds that

depredate aquaculture facilities in the southeastern United States), or to any question that involves the type of foraging habitat used by cormorants during specific times of the year.

The major implications of my research concerning Double-crested Cormorants relate to the management of this species to reduce aquaculture depredation. Aquaculture depredation is a relatively localized and seasonal issue, occurring primarily in the southeastern United States during the winter. While my research does not directly examine the efficacy of alternative management strategies, it does suggest that management of cormorants on the breeding grounds is not an efficient, effective, or warranted measure for reducing depredation at aquaculture facilities. Cormorants that winter at aquaculture facilities subsequently migrate to breeding colonies across the eastern United States, and while concentrations of these birds are highest in the western Great Lakes region, a substantial proportion of birds breeding outside of this region (e.g. approximately one third of the population breeding in Lake Champlain; Chapters 4 and 5) consume aquaculture resources during the winter. Furthermore, my observation that male cormorants are primarily responsible for aquaculture depredation suggests that management should target this sex, a prospect which is infeasible when managing sexually monomorphic adults on the breeding grounds. Given my findings, and the localized and seasonal manner of the conflict, I suggest that management of birds at aquaculture facilities is the only strategy for targeting birds contributing to depredation.

It is important for me to reiterate that the conclusions from my research apply to issues of cormorant management to reduce aquaculture depredation in the southeastern United States. Cormorants are managed for a number of other conflicts with humans and natural resources, including competition over commercial and sport fisheries, and degradation of terrestrial habitats across the species' migratory pathway (Chapter 4). My research does not relate to these conflicts,

and my conclusions, therefore, do not shed light on the necessity or efficacy of management to

address these issues.

COMPREHENSIVE REFERENCES

Amundsen, T., and J. Stokland. 1990. Egg size and parental quality influence nestling growth in the Shag. Auk 107:410–413.

Bauchinger, U., and S. McWilliams. 2009. Carbon Turnover in Tissues of a Passerine Bird: Allometry, Isotopic Clocks, and Phenotypic Flexibility in Organ Size. Physiological and Biochemical Zoology 82:787–797.

Bearhop, S., D. Thompson, S. Waldron, I. Russell, G. Alexander, and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. Journal of Applied Ecology 36:75–84.

Bearhop, S., G. Hilton, S. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society of London Series B-Biological Sciences 271:S215–S218.

Bearhop, S., R. A. Phillips, R. McGill, Y. Cherel, D. A. Dawson, and J. P. Croxall. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Pages 157–164. Marine Ecology Progress Series.

Bearhop, S., R. W. Furness, G. Hilton, S. Votier, and S. Waldron. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. Functional Ecology 17:270–275.

Ben-David, M., and D. M. Schell. 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. Oecologia 127:180–184.

Bildstein, K. L. 1993. White Ibis, wetland wanderer. Smithsonian Institution Press, Blue Ridge Summit, PA.

Blackwell, B. F., M. A. Stapanian, and D. C. Weseloh. 2002. Dynamics of the Double-crested Cormorant population on Lake Ontario. Wildlife Society Bulletin:345–353.

Bond, A. L., and A. W. Diamond. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecological Applications 21:1017–1023.

Bond, A., and I. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. Marine Ornithology 37:183–188.

Carleton, S. A., and C. Martínez del Rio. 2005. The effect of cold-induced increased metabolic rate on the rate of ^{13}C and ^{15}N incorporation in house sparrows (*Passer domesticus*). Oecologia 144:226–232.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors ($\Delta^{15}N$ and $\Delta^{13}C$): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

Chang, Y.-M., K. A. Hatch, T.-S. Ding, D. L. Eggett, H.-W. Yuan, and B. L. Roeder. 2008. Using stable isotopes to unravel and predict the origins of Great Cormorants (*Phalacrocorax carbo sinensis*) overwintering at Kinmen. Rapid Communications in Mass Spectrometry 22:1235–1244.

Chastant, J. E., D. T. King, D. V. C. Weseloh, and D. J. Moore. 2013. Population dynamics of Double-crested Cormorants in two interior breeding areas. The Journal of Wildlife Management 78:3–11.

Cherel, Y., K. A. Hobson, and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122:155–162.

Coulson, J., G. Potts, and J. Horobin. 1969. Variation in eggs of shag (*Phalacrocorax aristotelis*). Auk 86:232–&.

Craig, E. C. 2009. New York City Audubon's Harbor Herons Project: 2009 interim nesting survey. New York City Audubon, New York, NY.

Craig, E. C. 2013. New York City Audubon's Harbor Herons Project: 2013 nesting survey –28th annual report. New York City Audubon, New York, NY.

Craig, E. C., S. B. Elbin, J. A. Danoff-Burg, and M. I. Palmer. 2012. Impacts of Double-crested Cormorants (*Phalacrocorax auritus*) and other colonial waterbirds on plant and arthropod communities on islands in an urban estuary. Waterbirds 35 (special publication 1):4–12.

Cuthbert, F. J., L. R. Wires, and J. McKearnan. 2002. Potential impacts of nesting Double-crested Cormorants on Great Blue Herons and Black-crowned Night-Herons in the US Great Lakes region. Journal of Great Lakes Research 28:145–154.

Davis, W. E. and J. Kricher. 2000. Glossy Ibis (*Plegadis falcinellus*). No. 74 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

DeNiro, M., and S. Epstein. 1978. Influence of diet on distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506.

Diana, J. S., S. L. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. Journal of Great Lakes Research 32:306–320.

Dolbeer, R. 1991. Migration Patterns of Double-crested Cormorants East of the Rocky Mountains. Journal of Field Ornithology 62:83–93.

Dorr, B. S., L. W. Burger, and S. C. Barras. 2008. Evaluation of aerial cluster sampling of Double-crested Cormorants on aquaculture ponds in Mississippi. Journal of Wildlife Management 72:1634–1640.

Dorr, B. S., L. W. Burger, S. C. Barras, and K. C. Godwin. 2012*a*. Economic impact of Double-crested Cormorant, *Phalacrocorax auritus*, depredation on channel catfish, *Ictalurus punctatus*, aquaculture in Mississippi, USA. Journal of the World Aquaculture Society 43:502–513.

Dorr, B. S., S. L. Hanisch, P. H. Butchko, and D. G. Fielder. 2012*b*. Management of Double-crested Cormorants to improve sport fisheries in Michigan: three case studies. Human-Wildlife Interactions 6:155–168.

Doucette, J. L., B. Wissel, and C. M. Somers. 2010. Effects of lipid extraction and lipid normalization on stable carbon and nitrogen isotope ratios in Double-crested Cormorants: implications for food web studies. Waterbirds 33:273–284.

Doucette, J. L., B. Wissel, and C. M. Somers. 2011. Cormorant-fisheries conflicts: stable isotopes reveal a consistent niche for avian piscivores in diverse food webs. Ecological Applications 21:2987–3001.

Drent, R., A. D. Fox, and J. Stahl. 2006. Travelling to breed. Journal of Ornithology 147:122–134.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology

40:503–537.

France, R. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnology and Oceanography 40:1310–1313.

Glahn, J. F., and D. T. King. 2004. Bird depredation. Pages 1–27 *in* C. Tucker and J. Hargreaves, editors. Biology and culture of channel catfish. Elsiver, Amersterdam, The Netherlands.

Glahn, J. F., M. E. Tobin, and B. F. Blackwell. 2000*a*. A science-based initiative to manage Double-crested Cormorant damage to southern aquaculture. USDA National Wildlife Research Center - Staff Publications. Paper 532.

Glahn, J. F., M. E. Tobin, and J. B. Harrel. 1997. Possible effects of catfish exploitation on overwinter body condition of Double-crested Cormorants. Symposium on Double-crested Cormorants: population status and management issues in the Midwest Paper 11:107–113.

Glahn, J., and A. R. Stickley Jr. 1995. Wintering Double-crested Cormorants in the Delta region of Mississippi: population levels and their impact on the catfish industry. Colonial Waterbirds 18:137–142.

Glahn, J., and B. S. Dorr. 2002. Captive Double-crested Cormorant *Phalacrocorax auritus* predation on channel catfish *Ictalurus punctatus* fingerlings and its influence on single-batch cropping production. Journal of the World Aquaculture Society 33:85–93.

Glahn, J., and K. Brugger. 1995. The impact of Double-crested Cormorants on the Mississippi Delta catfish industry: A bioenergetics model. Colonial Waterbirds 18:168–175.

Glahn, J., and R. McCoy. 1995. Measurements of wintering Double-crested Cormorants and discriminant models of sex. Journal of Field Ornithology 66:299–304.

Glahn, J., D. Reinhold, and C. Sloan. 2000*b*. Recent population trends of Double-crested Cormorants wintering in the Delta region of Mississippi: responses to roost dispersal and removal under a recent depredation order. Waterbirds 23:38–44.

Glahn, J., P. Dixson, G. Littauer, and R. McCoy. 1995. Food habits of Double-crested Cormorants wintering in the Delta region of Mississippi. Colonial Waterbirds 18:158–167.

Glahn, J., S. J. Werner, T. Hanson, and C. Engle. 2002. Cormorant depredation losses and their prevention at catfish farms: economic considerations. Pages 138-146 *in* L. Clark, editor. Human conflicts with wildlife: economic considerations. Proceedings of the third NWRC special symposium, Fort Collins, CO, USA.

Good, T. P. 1998. Great Black-backed Gull (*Larus marinus*). No. 330 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Guillaumet, A., B. Dorr, G. Wang, J. D. Taylor, R. B. Chipman, H. Scherr, J. Bowman, K. F. Abraham, T. J. Doyle, and E. Cranker. 2011. Determinants of local and migratory movements of Great Lakes Double-crested Cormorants. Behavioral Ecology 22:1096– 1103.

Gunnarsson, T., J. Gill, J. Newton, P. Potts, and W. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. Proceedings of the Royal Society B-Biological Sciences 272:2319.

Harbor Herons Subcommittee. 2010. The Harbor Herons Conservation Plan- New York/New Jersey Harbor Region. S. B. Elbin and N. K. Tsipoura, editors. NY-NJ Harbor Estuary Program, New York, NY, USA.

Hatch, J. J. 1995. Changing populations of Double-crested Cormorants. Colonial Waterbirds 18:8–24.

Hatch, J. J. and D. V. C. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). No. 441 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hebert, C. E., D. V. C. Weseloh, A. Idrissi, M. T. Arts, and E. Roseman. 2009. Diets of aquatic birds reflect changes in the Lake Huron ecosystem. Aquatic Ecosystem Health & Management 12:37–44.

Hebert, C. E., J. Duffe, D. V. C. Weseloh, E. Senese, and G. Haffner. 2005. Unique island habitats may be threatened by Double-crested Cormorants. Journal of Wildlife Management 69:68–76.

Hebert, C. E., M. Bur, D. Sherman, and J. L. Shutt. 2008. Sulfur isotopes link overwinter habitat use and breeding condition in Double-crested Cormorants. Ecological Applications 18:561–567.

Hesslein, R. H., M. J. Capel, D. E. Fox, and K. A. Hallard. 1991. Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. Canadian Journal of Fisheries and Aquatic Sciences 48:2258–2265.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326.

Hobson, K. A. 2009. Trophic interactions between cormorants and fisheries: towards a more quantitative approach using stable isotopes. Waterbirds 32:481–490.

Hobson, K. A., and R. G. Clark. 1992*a*. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189–197.

Hobson, K. A., and R. G. Clark. 1992*b*. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94:181–188.

Hobson, K. A., K. Hughes, and P. Ewins. 1997. Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. Auk 114:467–478.

Hothem, L. R., B. E. Brussee and W. E. Davis. 2010. Black-crowned Night-Heron (*Nyctocorax nycticorax*). No. 74 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

Inger, R., X. Harrison, G. Ruxton, J. Newton, K. Colhoun, G. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop. 2010. Carry‐over effects reveal reproductive costs in a long‐distance migrant. Journal of Animal Ecology 79:974–982.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

Johnsgard, P. 1993. Cormorants, darters, and pelicans of the world. Smithsonian Institution Press, Washington.

King, D. T., B. Blackwell, B. Dorr, and J. L. Belant. 2010. Effects of aquaculture on migration and movement patterns of Double-crested Cormorants. Human-Wildlife Conflicts 4:77–86.

King, D. T., B. K. Strickland, and A. A. Radomski. 2012*a*. Winter and summer home ranges and core use areas of Double-crested Cormorants captured near aquaculture facilities in the southeastern United States. Waterbirds 35:124–131.

King, D. T., B. K. Strickland, and A. Radomski. 2012*b*. Migration patterns of Double-crested Cormorants wintering in the southeastern United States. Waterbirds 35:132–137.

King, D., J. Glahn, and K. Andrews. 1995. Daily activity budgets and movements of winter roosting Double-crested Cormorants determined by biotelemetry in the Delta region of Mississippi. Colonial Waterbirds 18:152–157.

King, D., J. Paulson, D. Leblanc, and K. Bruce. 1998. Two capture techniques for American White Pelicans and Great Blue Herons. Colonial Waterbirds 21:258–260.

Kolb, G. S., L. Jerling, C. Essenberg, C. Palmborg, and P. A. Hambäck. 2012. The impact of nesting cormorants on plant and arthropod diversity. Ecography 35:726–740.

Kushlan, J. A. 2012. A history of conserving colonial waterbirds in the United States. Waterbirds 35:608–625.

Logan, J. M., T. D. Jardine, T. J. Miller, S. E. Bunn, R. A. Cunjak, and M. E. Lutcavage. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. Journal of Animal Ecology 77:838–846.

Lott, C. A., T. Meehan, and J. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. Oecologia 134:505–510.

Macko, S. A., M. L. Fogel Estep, M. H. Engel, and P. E. Hare. 1986. Kinetic fractionation of stable nitrogen isotopes during amino acid transamination. Geochimica et Cosmochimica Acta 50:2143–2146.

McCrimmon Jr., D. A., J. C. Ogden, and G. T. Bancroft. 2001. Great Egret (*Ardea alba*). No. 570 *in* A. Poole editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Mizutani, H., M. Fukuda, Y. Kabaya, and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk 107:400–403.

Nettleton, J. A., and J. Exler. 1992. Nutrients in wild and farmed fish and shellfish. Journal of Food Science 57:257–260.

Neuman, J., D. Pearl, P. Ewins, R. Black, D. V. C. Weseloh, M. Pike, and K. Karwowski. 1997. Spatial and temporal variation in the diet of double-crested cormorants (Phalacrocorax auritus) breeding on the lower Great Lakes in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 54:1569–1584.

New York State Department of Environmental Conservation. 2014. New York species of greatest conservation need. <http://www.dec.ny.gov/docs/wildlife_pdf/sgcnlist.pdf>. Downloaded January 2015.

Newsome, S. D., C. Martínez del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429–436.

Norris, D. 2006. Vertebrate Endocrinology. Pages 313–314. Fourth edition. Elsevier Academic Press.

Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. Condor 109:535–547.

Norris, D. R., P. P. Marra, R. Montgomerie, T. K. Kyser, and L. Ratcliffe. 2004. Reproductive effort, molting latitude, and feather color in a migratory songbird. Science 306:2249.

Ofukany, A., K. Hobson, and L. I. Wassenaar. 2012. Connecting breeding and wintering habitats of migratory piscivorous birds: implications for tracking contaminants (Hg) using multiple stable isotopes. Environmental Science & Technology 46:3253–3262.

Oppel, S., and A. N. Powell. 2008. Assigning King Eiders to wintering regions in the Bering Sea using stable isotopes of feathers and claws. Marine Ecology Progress Series 373:149–156.

Parnell, J. F., D. G. Ainley, H. Blokpoel, B. Cain, T. W. Custer, J. L. Dusi, S. Kress, J. A. Kushlan, W. E. Southern, and L. E. Stenzel. 1988. Colonial waterbird management in North America. Colonial Waterbirds 11:129–169.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in Herring Gulls (*Larus argentatus*). Nature 228:1221–1222.

Peterson, B., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology And Systematics 18:293–320.

Phillips, D. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 127:166–170.

Pierotti, R. and T. P. Good. 1994. Herring Gull (*Larus argentatus*). No. 124 *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA.

Post, D. 2002*a*. The long and short of food-chain length. Trends in Ecology & Evolution 17:269–277.

Post, D. M. 2002*b*. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Quintana, F., R. Wilson, P. DellArciprete, E. Shepard, and A. G. Laich. 2010. Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant *Phalacrocorax atriceps* a colonial seabird. Oikos 120:350–358.

Reudink, M. W., C. E. Studds, P. P. Marra, T. K. Kyser, and L. M. Ratcliffe. 2009a. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American Redstart *Setophaga ruticilla*. Journal of Avian Biology 40:34–41.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009b. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society B-Biological Sciences 276:1619–1626.

Ridgway, M. S., J. B. Pollard, and D. V. C. Weseloh. 2006. Density-dependent growth of Double-crested Cormorant colonies on Lake Huron. Canadian Journal Of Zoology-Revue Canadienne De Zoologie 84:1409–1420.

Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology & Evolution 19:256–263.

Rudstam, L., A. VanDeValk, C. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14:149–163.

R Development Core Team 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Downloaded September 2014.

SAS Institute. 2013. JMP statistical discovery software. Eleventh edition. SAS institute, Cary, NC.

Scherr, H., J. Bowman, and K. F. Abraham. 2010. Migration and winter movements of Double-crested Cormorants breeding in Georgian Bay, Ontario. Waterbirds 33:451–460.

Sears, J., S. A. Hatch, and D. M. O'Brien. 2008. Disentangling effects of growth and nutritional status on seabird stable isotope ratios. Oecologia 159:41–48.

Somers, C. M., J. L. Doucette, D. V. C. Weseloh, V. A. Kjoss, and R. M. Brigham. 2011. Interactions between Double-crested Cormorants and other ground-nesting species. Waterbirds 34:168–176.

Somers, C. M., M. N. Lozer, and J. S. Quinn. 2007. Interactions between Double-crested Cormorants and Herring Gulls at a shared breeding site. Waterbirds 30:241–250.

Steele, K. W., and R. M. Daniel. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. Journal of Agricultural Science 90:7–9.

Stokland, J., and T. Amundsen. 1988. Initial size hierarchy in broods of the shag - relative significance of egg size and hatching asynchrony. Auk 105:308–315.

Taylor, J., and B. S. Dorr. 2003. Double-crested Cormorant impacts to commercial and natural resources. Wildlife Damage Management Conference 10:43–51.

Tobin, M. E., D. T. King, B. S. Dorr, S. J. Werner, and D. S. Reinhold. 2002. Effect of roost harassment on cormorant movements and roosting in the delta region of Mississippi. Waterbirds 25:44–51.

Van Eerden, M. R., and M. Munsterman. 1995. Sex and age-dependent distribution in wintering cormorants *Phalacrocorax carbo sinensis* in western Europe. Ardea 83:285–297.

Vanderklift, M., and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia 136:169–182.

Vasil, C. A., M. J. Polito, W. P. Patterson, and S. D. Emslie. 2012. Wanted: dead or alive? Isotopic analysis ($\delta13C$ and $\delta15N$) of *Pygoscelis* penguin chick tissues supports opportunistic sampling. Rapid Communications in Mass Spectrometry 26:487–493.

Webster, M., P. P. Marra, S. Haig, S. Bensch, and R. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

Weseloh, D. V. C., C. Pekarik, T. Havelka, G. Barrett, and J. Reid. 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. Journal of Great Lakes Research 28:125–144.

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the Double-crested Cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. Waterbirds 29:9–37.