

AN ABSTRACT OF THE THESIS OF

Cynthia D. Anderson for the degree of Master of Science in Wildlife Science. Presented on October 21, 2002.

Title: Factors Affecting Colony Size, Reproductive Success, and Foraging Patterns of Double-crested Cormorants Nesting on East Sand Island in the Columbia River Estuary.

Abstract approved: _____

Daniel D. Roby

The purpose of this study was to investigate the primary factors affecting colony size, reproductive success, and foraging patterns of Double-crested Cormorants (*Phalacrocorax auritus albociliatus*) nesting at East Sand Island in the Columbia River estuary, the largest colony of this species on the Pacific Coast of North America. This colony grew dramatically over the past 13 years and appears to represent a substantial proportion (>40%) of the West Coast population. Due to increasing concern over avian predation on juvenile salmonids in the Columbia River estuary, there was a need to understand the factors limiting the size and productivity of this large and growing cormorant colony and how breeding adults exploit the available forage fish resources in the estuary.

The East Sand Island colony recently fragmented into separate sub-colonies that differed in reproductive success; clutch size, hatching success, brood size at fledging, nesting success, and overall productivity were all higher at a recently-formed satellite sub-colony compared to the main colony. Depredation of cormorant nest contents by Glaucous-winged/Western Gulls (*Larus glaucescens* X *L. occidentalis*) following disturbances caused by Bald Eagles (*Haliaeetus leucocephalus*) appeared to be the primary factor limiting reproductive success. During my study, nesting habitat and food supply did not appear to be limiting colony size or reproductive success. I predict that the colony will continue to expand unless forage fish stocks decline and/or eagle disturbances increase.

I used radio-telemetry to investigate the spatial and temporal patterns of foraging male and female Double-crested Cormorants. Nesting adults tended to commute over 5 km from the colony to forage in either the estuarine-mixing zone or the freshwater zone of the estuary, where forage fishes were presumably more available than in the marine zone near the colony. The sexes exhibited striking differences in foraging distribution. Males commuted longer distances to forage in the freshwater zone compared to females, which tended to forage in the estuarine-mixing zone; however, females took longer foraging trips than males on average. Gender differences in foraging patterns may enhance the foraging efficiency of pairs nesting at a large colony such as East Sand Island. The

cormorant breeding colony on East Sand Island seems to be avoiding density-dependent constraints of food supply by foraging over a wide area of the estuary on a diversity of marine forage fishes whose stocks are currently high. I predict that in years when stocks of marine forage fish within the estuary are low (e.g., due to poor ocean conditions), Double-crested Cormorants may become more reliant on the more predictable fish resources of the estuary, such as out-migrating salmonid smolts.

Factors Affecting Colony Size, Reproductive Success, and Foraging
Patterns of Double-crested Cormorants Nesting on East Sand Island
in the Columbia River Estuary

by

Cynthia D. Anderson

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented October 21, 2002
Commencement June 2003

ACKNOWLEDGEMENTS

The research presented in this thesis was funded by the Bonneville Power Administration (BPA) Contract 97BI33475. I thank Oregon State University and the Department of Fisheries and Wildlife for administrative support. In particular, I wish to thank: Ellen Holsberry and Jane Toliver for their help keeping the project running smoothly, Jill Anderson, Lavon Mauer, and Charlotte Vickers for being my graduate school “survival guides”, Jan Cyrus and Valerie Rosenburg for keeping me out of INS trouble, and Janet Webster and the rest of the HMSC library staff for their cheerful assistance.

I thank Bergmann Photographic Services Inc. (Portland, Oregon) for the aerial photographs of the East Sand Island cormorant colony and the Photogrammetry Department at BPA (Vancouver, Washington) for the analysis of the photographs to estimate colony size. My thesis work would not have been possible without the equipment, services, or logistical support provided by: Ken Collis, Geoff Dorsey, Ben Lakey, Ray Ronald, Kim Salarzon, and Eric Stone, for which I am grateful. Special thanks go to Captain Ted for his flexibility and endurance during the aerial telemetry surveys.

Data collection for this work was conducted by numerous, dedicated technicians and volunteers. I am indebted to each of them for

their efforts and enthusiasm in the field. Cormorant data collection was assisted by: Michelle Antolos, Naomi Bargmann, Bobby Begay, Eli Bridge, Heather Christie, Chris Couch, Cristina Faustino, Adrian Gall, Kristen Gorman, Mike Layes, Stacey Lehmann, Tyler Lewis, Cara Lindsey, Doug Lynch, Shari McDougal, Doug Robinson, Ian Rose, Jeff Rosier, Nick Spang, Melissa Thompson, Jason Wolf, and Sadie Wright. Jessica Adkins, Scott Anderson, Nate Chelgren, Don Lyons, Anne-Mary Myers, Kelly Redman, and Rob Suryan deserve special thanks for their steadfast support and willingness to lend a hand.

I am sincerely indebted to: Scott Anderson, Ken Collis, Mike Hawbecker, Selina Heppell, Pat Jodice, Don Lyons, and Rob Suryan for their time, insights, perspectives, and expertise. Micheal Chutter, Alan Clark, David Craig, Gary Ivey, Roy Lowe, Kathy Molina, Maura Naughton, Mark Rauzon, and Ulrich Wilson provided invaluable comments and unpublished data regarding Pacific coast Double-crested Cormorant populations. Bob Anthony and Frank Isaacs provided a wealth of knowledge and unpublished data on Bald Eagle populations in Oregon. Bob Emmett happily took time to discuss the behaviour of Columbia River fishes with me. Lisa Ganio, Manuela Huso, and Cliff Pereira all provided statistical advice. Jessica Adkins and Anne-Mary Myers were responsible for the cormorant diet analyses. Ken Collis, Pat Jodice, Kim Nelson, Dan

Roby, and Rob Suryan provided helpful comments that improved earlier drafts of one or both of the manuscripts in this thesis.

My graduate committee members, Sue Haig and Cliff Pereira, have been helpful and supportive, for which I am grateful. I am deeply grateful to Dan Roby, my major advisor and mentor, for his enthusiasm, invaluable guidance, and unwavering support throughout this process.

I thank Grant Gilchrist and Kathy Turco whose words of wisdom unwittingly convinced me to go back to school. I thank my family and friends who supported my decision to get my MS, and to go across the continent and to the States to get it. I am also grateful to my friends, avian lab-mates, and fellow Roby-ites that became my family and support group throughout this degree, especially: Jessica Adkins, Jill Anderson, Maya Anderson, Scott Anderson, Michelle Antolos, Marlene Bellmann, Karl Chelgren, Emily Chelgren, Rosie Chelgren, Peggy Chelgren-Smith, Adrian Gall, Doug Milek, Anna Noson, Derek Risso, Dan Rizzolo, John Siegle, and Rob Suryan. Finally, I thank Nate Chelgren for his love, unflagging support, insightful comments, field assistance, programming expertise, and statistical advice. You have been vital, in every way, to the completion and success of this thesis. Thank you, Nater, for your faith in me, and your firm encouragement to, “cut through the CRAPP”.

CONTRIBUTION OF AUTHORS

Daniel D. Roby's involvement in the development and completion of this thesis was integral; Dan secured funding for this research, assisted in the development of the ideas for each manuscript, and thoroughly edited each manuscript. Nathan D. Chelgren provided crucial statistical and programming advice for the second chapter.

TABLE OF CONTENTS

	<u>Page</u>
Chapter 1. GENERAL INTRODUCTION.....	1
Chapter 2. FACTORS AFFECTING COLONY SIZE AND REPRODUCTIVE SUCCESS OF DOUBLE-CRESTED CORMORANTS NESTING ON EAST SAND ISLAND IN THE COLUMBIA RIVER ESTUARY.....	7
Abstract.....	8
Introduction.....	9
Methods.....	15
Results.....	26
Discussion.....	37
Literature Cited.....	50
Chapter 3. FORAGING PATTERNS OF MALE AND FEMALE DOUBLE-CRESTED CORMORANTS NESTING IN THE COLUMBIA RIVER ESTUARY	60
Abstract.....	61
Introduction.....	62
Methods.....	67
Results.....	79
Discussion.....	86
Literature Cited.....	101
Chapter 4. SYNOPSIS AND CONCLUSIONS.....	109
BIBLIOGRAPHY.....	113

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1.1 Estimated annual population growth rate (λ) of the nesting colony of Double-crested Cormorants at East Sand Island, 1989-2002.....	28
1.2 Reproductive success of Double-crested Cormorants nesting in main and satellite sub-colonies on East Sand Island in 2001. Averages are expressed as mean \pm SE.....	31
1.3 Poisson log-linear regression model for factors affecting the productivity of Double-crested Cormorant nests during the 2001 nesting season.....	33
1.4 Observed disturbance events at the East Sand Island Double-crested Cormorant colony in 2001. Averages are expressed as mean \pm SE. A disturbance event was defined as any event that caused the majority of nesting adults, in one or both of the monitored sub-colonies, to display visible signs of attention to an external stimulus.....	35
2.1 Average foraging trip duration (hrs; A), time spent foraging (hrs/d; B) and frequency of trips (trips/d; C) for male and female Double-crested Cormorants nesting on East Sand Island during June and July of 2001. Results of two-way repeated measures ANOVAs are expressed as means \pm SE. NB: day unit refers to the 18-hr daytime period (04:00 – 22:00) considered for these analyses.....	87
2.2 Separate split-plot-in-time ANOVAs for each factorial effect of time of day, tide stage, and tide series on the proportion of time actively-nesting Double-crested Cormorants spent off-colony (presumably foraging) during June of 2001. Error terms are shown in italics below each set of factorial effects.....	88

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1.1 Map of study area (dotted rectangle) on the west end of East Sand Island in Clatsop County, Oregon in the Columbia River estuary.....	17
1.2 Locations of sub-colonies (black polygons) of nesting Double-crested Cormorants on the west end of East Sand Island (shown in gray) during 1997 (above) and 2001 (below). Schematics are based on aerial photographs taken during mid-incubation each year. The satellite sub-colony (dotted circle) and the main sub-colony (dotted rectangle), observation blinds (black squares), and above-ground tunnel system (double-lines) are also shown.....	18
1.3 Estimated number of pairs (\pm SE) of Double-crested Cormorants nesting on East Sand Island, 1989-2001. (Linear regression: $F_{1,8} = 3062$, $r^2 = 0.997$, $P < 0.0001$).....	27
1.4 Estimated average productivity (young fledged/nesting pair) of Double-crested Cormorants nesting on East Sand Island, 1997-2001 (no estimate available for 1999). Numbers of nests monitored in each year are shown in parentheses.....	29
1.5 Percent of total disturbance events ($N = 166$) caused by Bald Eagles (gray bars), human activity (black bars), and unknown causes (white bars) observed for Double-crested Cormorants nesting at East Sand Island in 2001.....	36
1.6 Intensity of reactions exhibited by nesting Double-crested Cormorants in response to Bald Eagle disturbances ($N = 72$) at a main sub-colony (black bars) and at a satellite sub-colony (gray bars) on East Sand Island in 2001. (Multinomial distribution for ordinal data: $\chi^2_1 = 9.20$, $P = 0.0024$).....	37

LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
2.1 Map of the study area indicating the aerial telemetry survey area (dotted rectangle) searched for foraging radio-tagged Double-crested Cormorants nesting on East Sand Island (double-lined square) in the Columbia River estuary.....	69
2.2 Salinity gradient for the Columbia River estuary, showing marine zone (stripes), estuarine-mixing zone (dotted), and freshwater zone (gray) (defined by Simenstad et al. 1990).....	70
2.3 Aerial telemetry relocations of male (cross, $N = 125$) and female (circle, $N = 61$) Double-crested Cormorants actively-nesting on East Sand Island (double-lined rectangle). Surveys were conducted throughout the Columbia River estuary between 1 June and 26 July, in 2000 ($N = 138$ relocations) and 2001 ($N = 48$ relocations).....	80
2.4 Proportion of total off-colony relocations for female ($N = 61$) and male ($N = 125$) radio-tagged Double-crested Cormorants in each 5-km interval (straight-line distance) from the nesting colony on East Sand Island in the Columbia River estuary. All relocations were from aerial telemetry surveys conducted during the 2000 and 2001 nesting seasons.....	83
2.5 Distribution of aerial telemetry relocations for two individual radio-tagged Double-crested Cormorants (6 relocations for one female shown as solid circles and 5 relocations for one male shown as crosses) actively-nesting at East Sand Island (double-lined rectangle) in the Columbia River estuary.....	84

LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
2.6 Proportion of time spent off-colony (and presumably foraging) in June of 2001 for radio-tagged Double-crested Cormorants actively-nesting on East Sand Island during neap (A) and spring (B) tide series by time of day and tide stage. Proportion of time off-colony is expressed as the proportion of detection cycles when a transmitter was not detected for at least 2 consecutive scanning cycles by on-colony receiving stations for each combination of time of day, tide stage, and tidal series.....	89
2.7 Diet composition (mean % identifiable fish biomass) of collected female ($N = 25$) and male ($N = 40$) Double-crested Cormorants nesting at East Sand Island in June of 2000 and 2001 (D. Roby, unpubl. data).....	93

DEDICATION

To my Grandma, Alma Jay, who in her 91st year is my most vibrant mentor,
and to my late uncle, Bill Jay, who taught me to live for today.

Factors Affecting Colony Size, Reproductive Success, and Foraging
Patterns of Double-crested Cormorants Nesting on East Sand Island
in the Columbia River Estuary

CHAPTER 1

GENERAL INTRODUCTION

We sought to determine the primary factors affecting the reproductive success and foraging patterns at the large nesting colony of Double-crested Cormorants (*Phalacrocorax auritus*) on East Sand Island in the Columbia River Estuary for three main reasons. First, the nesting season of these piscivorous waterbirds coincides with peak out-migration of juvenile salmonids (*Oncorhynchus* spp.) from the Columbia River basin (FPC 2002). Cormorant predation in the estuary may be a significant source of mortality for migrating smolts, many of which are listed as either threatened or endangered under the U.S. Endangered Species Act (ESA; NMFS 2002). Second, the East Sand Island nesting colony of Double-crested Cormorants likely represents a substantial proportion of the West Coast population (Carter et al. 1995), which may be experiencing declines (Tyson et al. 1999, Wires et al. 2001). Finally, a recent Draft Environmental Impact Statement proposed to manage and control the breeding and wintering populations of Double-crested Cormorants throughout the contiguous U.S. (USFWS 2001).

The Double-crested Cormorant (*Phalacrocorax auritus*) has the widest range of the six species of cormorants breeding in North America (Hatch 1995). There are five subspecies of Double-crested Cormorants that are differentiated by size, crest characters, and regional distribution; cormorants are sexually dimorphic, with males averaging larger than females (Hatch 1995, Hatch and Weseloh 1999). Double-crested Cormorants are apparently socially monogamous, biparental, territorial breeders that nest colonially (10's to 1000's of nests) that generally show high natal philopatry at colony sites that are free of ground predators and close to feeding areas (Hatch and Weseloh 1999). Nests are constructed on a variety of substrates, including in trees, on navigational aids, on cliffs, and on the ground. They typically first breed at 3 yrs of age, lay large clutches (3-7 eggs), and have a mean life expectancy of about 6 yrs (Hatch and Weseloh 1999).

Numbers of Double-crested Cormorants (*P. a. auritus*) have increased dramatically across most of North America during the last 30 years (Hatch 1995, Sauer et al. 1997, Hatch and Weseloh 1999). There is evidence, however, that the West Coast population (*P. a. albociliatus*) may have declined in recent years (Carter et al. 1995, Wires et al. 2001), especially in the Pacific Northwest (USFWS, unpubl. data, Conservation Data Centre 2002). In contrast to declines in numbers of *P. a. albociliatus* nesting at other colonies along the coast of the Pacific Northwest, the East

Sand Island colony during the early to mid 1990s (Carter et al. 1995, Collis et al. 2002). Immigration from other colonies occurred to the extent that the East Sand Island colony became the largest Double-crested Cormorant colony on the Pacific Coast of North America (Carter et al. 1995). We examined commonly cited factors limiting the size and productivity of seabird colonies to identify the most important constraints on colony size and reproductive success of cormorants nesting on East Sand Island. We hypothesized that after the rapid expansion of the cormorant colony on East Sand Island in the early to mid-1990s, colony size has likely stabilized due to density-dependent effects on the availability of both food and nest sites.

The Double-crested Cormorants nesting on East Sand Island share the island with >40,000 other nesting and roosting piscivorous birds (e.g., terns, gulls, pelicans; D. Roby, unpubl. data). Intense feeding activity of this large and growing colony of cormorants and other piscivores may lead to prey-depletion around the nesting colony (Ashmole 1963, Furness and Birkhead 1984, Birt et al. 1987). We predicted that the cormorants nesting at East Sand Island would maximize foraging efficiency by foraging as close to the colony as intraspecific competition allows. Due to density-dependent effects, we predicted that cormorants would: 1) take longer foraging trips, 2) take fewer foraging trips, and 3) spend more total time foraging per day than Double-crested Cormorants nesting at other colonies that have been the subject of published studies (Fowle 1997).

We sought to understand which environmental factors (e.g., diurnal and tidal cycles) predominately influenced the spatial and temporal patterns of foraging exhibited by male and female Double-crested Cormorants nesting at East Sand Island.

Due to the growing concern over avian predation on juvenile salmonids in the Columbia River estuary, there is a need to investigate how this large cormorant colony exploits the available forage fish resources of the estuary in order to understand predation rates on juvenile salmonids by cormorants nesting on East Sand Island. Furthermore, there is a need to understand how East Sand Island cormorants are able to meet their resource needs while other Double-crested Cormorant colonies along the coast of the Pacific Northwest.

Literature Cited

- Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-473.
- Birt, V.L, T.P. Birt, D. Goulet, D.K. Cairns, and W.A. Montevecchi. 1987. Ashmole's halo: Direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40:205-208.
- Carter, H.R., A.L. Sowls, M.S. Rodway, U.W. Wilson, R.W. Lowe, G.J. McChesney, F. Gress, and D.L. Anderson. 1995. Population size, trends, and conservation problems of the Double-crested Cormorant on the Pacific Coast of North America. *Colonial Waterbirds* 18 (Special Publication 1):189-215.
- Collis, K., D.D. Roby, D.P. Craig, S.L. Adamany, J.Y. Adkins, and D.E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537-550.
- Conservation Data Centre. 2002. RED and BLUE LISTS for British Columbia amphibians, reptiles, birds, and mammals. At <http://srmwww.gov.bc.ca/cdc/tracking.htm>.
- Fowle, M.R. 1997. Population dynamics, food habits, and bioenergetics of Double-crested Cormorants in Lake Champlain. M.S. thesis, University of Vermont, Burlington, VT.
- FPC (Fish Passage Center). 2002. Archived juvenile salmonid passage counts for 2000 and 2001. At <http://www.fpc.org/SMPDATA.html>.
- Furness, R.W., and T.R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655-656.
- Hatch, J.J. 1995. Changing populations of Double-crested Cormorants. *Colonial Waterbirds* 18 (Special Publication 1):8-24.
- Hatch, J.J., and D.V. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). In *The Birds of North America*, No. 441 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA. 36 pp.

- NMFS (National Marine Fisheries Service). 2002. Endangered Species Act status of west coast salmonids. NMFS, Northwest Region, Portland, OR. At <http://www.nwr.noaa.gov>.
- Sauer, J.R., J.E. Hines, G. Gough, I. Thomas, and B.G. Peterjohn. 1997. The North American breeding bird survey results and analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, MD. At www.mbr-pwrc.usgs.gov/bbs/.
- Tyson, L.A., J.L. Belant, F.J. Cuthbert, and D.V. Weseloh. 1999. Nesting populations of Double-crested Cormorants in the United States and Canada. Pages 17-26 *in* M.E. Tobin (ed.), Symposium on Double-crested Cormorants: population status and management issues in the Mid-west. USDA/APHIS Tech. Bull. No. 1879. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Washington, DC. 164 pp.
- USFWS (United States Fish and Wildlife Service). 2001. Draft environmental impact statement: Double-crested Cormorant management. United States Department of the Interior, Fish and Wildlife Service, Washington, DC. 152 pp.
- Wires, L.R., F.J. Cuthbert, D.R. Trexel, and A.R. Joshi. 2001. Status of the Double-crested Cormorant (*Phalacrocorax auritus*) in North America. Final Report to United States Fish and Wildlife Service. University of Minnesota, St. Paul, MN. 360 pp.

CHAPTER 2

FACTORS AFFECTING COLONY SIZE AND REPRODUCTIVE
SUCCESS OF DOUBLE-CRESTED CORMORANTS NESTING ON
EAST SAND ISLAND IN THE COLUMBIA RIVER ESTUARY

Cynthia D. Anderson and Daniel D. Roby

Abstract

We investigated factors that potentially limit the size and reproductive success of a nesting colony of Double-crested Cormorants (*Phalacrocorax auritus albociliatus*) on East Sand Island in the Columbia River estuary, Oregon. In contrast to declines in numbers of *P. a. albociliatus* nesting at other colonies along the coast of the Pacific Northwest, the East Sand Island colony has grown dramatically in the last 13 years from less than 100 pairs in 1989 (R. Lowe, USFWS, pers. comm.) to over 8,500 breeding pairs in 2002. Immigration from other colonies has occurred to the extent that the East Sand Island colony is now the largest Double-crested Cormorant colony on the Pacific Coast of North America. Recent fragmentation of the East Sand Island colony has led to separate sub-colonies that differ in reproductive success; overall productivity averaged higher at a recently formed satellite sub-colony compared to a main sub-colony. Productivity was positively correlated with distance from gull nesting areas, regardless of sub-colony. Depredation of cormorant nest contents by Glaucous-winged/Western Gulls (*Larus glaucescens* X *L. occidentalis*) following disturbances caused by Bald Eagles (*Haliaeetus leucocephalus*) appeared to be the primary factor limiting reproductive success. The high productivity of this colony suggests that food availability was high during the study. The colony is likely to continue to expand unless forage fish stocks decline and/or eagle disturbances increase.

Introduction

The Double-crested Cormorant (*Phalacrocorax auritus*) has the widest range of the six species of cormorants breeding in North America (Hatch 1995). There are five subspecies of Double-crested Cormorants that are differentiated by size, crest characters, and regional distribution (Hatch 1995, Hatch and Weseloh 1999). Double-crested Cormorants are colonial nesters (10's to 1000's of nests) that generally show high natal philopatry at colony sites that are free of ground predators and close to feeding areas (Hatch and Weseloh 1999). Nests are constructed on a variety of substrates, including in trees, on navigational aids, on cliffs, and on the ground. They typically first breed at 3 yrs of age, lay large clutches (3-7 eggs), and have a mean life expectancy of about 6 yrs (Hatch and Weseloh 1999).

Numbers of Double-crested Cormorants have increased dramatically across most of North America during the last 30 years (Hatch 1995, Sauer et al. 1997, Hatch and Weseloh 1999). There is growing evidence, however, that the overall rate of increase in some populations has declined over the past decade (Tyson et al. 1999). In some regions of North America, such as the Pacific Coast, Double-crested Cormorants may have actually declined in recent years (Carter et al. 1995, Wires et al. 2001). Double-crested Cormorants nesting along the Pacific Coast of North America are recognized as two subspecies: the West Coast

subspecies (*P. a. albociliatus*) and the Alaska subspecies (*P. a. cincinatus*).

Members of the West Coast subspecies breed along the Pacific coast of North America from southern British Columbia to Sinaloa, Mexico (Carter et al. 1995, Cannings 1998). There is evidence that this subspecies may be undergoing a range-wide decline. In Baja California, Mexico, Isla San Martín was once considered the largest nesting colony of Double-crested Cormorants on the west coast of North America (ca. 350,000 pairs, Wright 1913); however, this colony has declined dramatically in numbers and is currently estimated at ca. 600 pairs (Palacios and Mellink 2000). Formerly large colonies of Double-crested Cormorants in California have also experienced declines. For example, over 5,000 pairs of Double-crested Cormorants nested on Mullet Island in the Salton Sea National Wildlife Refuge (NWR) as recently as 1999 (D. Shuford, Point Reyes Bird Observatory, pers. comm.), yet the colony was abandoned in 2001 (K. Molina, National History Museum of Los Angeles County, pers. comm.).

Similar trends have been documented over most of the Pacific Northwest. In British Columbia, the numbers of breeding Double-crested Cormorants have declined markedly and the species is currently designated as Threatened on the provincial Red List (Conservation Data Centre 2002). Colonies along the Washington coast have exhibited striking declines, with the total breeding population on the outer coast of

Washington declining by 80% over the past decade (U. Wilson, USFWS, unpubl. data.). In Oregon, most of the documented inland colonies have declined or been abandoned (USFWS, unpubl. data.), possibly due to emigration to coastal colonies (Carter et al. 1995). Supporting the hypothesis that breeding adults have emigrated from coastal British Columbia and Washington, as well as interior Oregon, the colony on East Sand Island in the Columbia River estuary grew rapidly from less than 100 pairs in 1989 (R. Lowe, USFWS, pers. comm.) to over 2,000 breeding pairs in 1991 (Carter et al. 1995). Currently, East Sand Island supports the largest known Double-crested Cormorant colony on the Pacific Coast of North America (Carter et al. 1995, Collis et al. 2002).

Several factors are blamed for recent declines in size and reproductive success of some colonies of Double-crested Cormorants in the Pacific Northwest (e.g., Great Chain, Five Finger, and Mandarti Islands, BC; Juan de Fuca Strait Islands, WA; Sheepy Lake, Lower Klamath Lake NWR, OR). One factor is reduction in forage fish abundance due to El Niño events (Wilson 1991) and ocean regime shifts (Emmett and Brodeur 2000). Additional factors include habitat loss due to agricultural and water developments (Carter et al. 1995), and increases in disturbances at nesting colonies from Bald Eagle (*Haliaeetus leucocephalus*) and humans (Verbeek 1982, Rodway 1991, Moul 1996, Moul 2000, Moul and Gebauer 2002).

Food availability (Ashmole 1963, Lack 1967, Furness and Birkhead 1984, Birt et al. 1987, Cairns 1992) and availability of quality nest sites (Wittenberger and Hunt 1985, Furness and Monaghan 1987, Ainley and Boekelheide 1990) are generally considered to be the prevailing factors limiting seabird reproductive success. In addition, predation pressure, both direct (predation on adults, eggs, and nestlings) and indirect (disturbances to nesting birds that expose nest contents to depredation), is recognized as a major factor influencing nest site selection and colony structure (Kruuk 1964, Paine et al. 1990, Siegel-Causey and Kharitonov 1990, Parrish et al. 2001).

Numerous studies have examined the influence of various nest characteristics on reproductive success of seabirds, including nest initiation date, distance of the nest from the edge of the colony, nest elevation, and nesting habitat (e.g., Coulson 1968, McNeil and Léger 1987, Good 2002). Results vary considerably, however, highlighting the complexity of the costs and benefits incurred from colonial nesting (Wittenberger and Hunt 1985, Clode 1993, Rolland et al. 1998). For example, early nest initiation has been cited frequently as a characteristic associated with high reproductive success in colonial seabirds (Birkhead 1977, Aebischer 1986, McNeil and Léger 1987). Yet there may be fitness benefits for parents that initiate nests during the peak (Hatchwell 1991).

Nest density, often measured using nearest neighbour distance, has been identified as a factor affecting reproductive success in seabird

colonies (Birkhead 1977, Furness 1984, Anderson and Hodum 1993). A study of shags (*P. aristotelis*) reported that productivity was negatively correlated with nest density where high-quality nest sites were limited (Potts et al. 1980). In contrast, Siegel-Causey and Hunt (1981) determined that nest predators depredated more Double-crested Cormorant nests at intermediate nest densities. Furthermore, acquiring a central nest site farther from the colony edge is generally associated with higher reproductive success in most seabirds (Coulson 1968, DesGranges and Reed 1981, Siegel-Causey and Hunt 1986, Léger and McNeil 1987, Regehr et al. 1998, Andrews and Day 1999, but see Brunton 1977). Increased nest predation is considered to be a primary cause of decreased reproductive success for pairs nesting near the edge (Hamilton 1971, Spear 1993).

Previous studies have shown that seabirds nesting in various habitat types and locations within the colony may experience large differences in reproductive success, often due to differences in exposure to nest predators (Siegel-Causey and Hunt 1981, Léger and McNeil 1987, Hatchwell 1991, Parrish 1995, Rowe and Jones 2000, Good 2002). For example, cormorants nesting on steeper slopes or elevated platforms had greater reproductive success, presumably due to better detection of approaching avian predators (Lewis 1929, Siegel-Causey and Hunt 1981, but see Léger and McNeil 1987). Other studies have shown that seabirds nesting in exposed areas of a colony are more likely to leave their nests

during disturbances by avian predators, and consequently experience lower reproductive success than conspecifics nesting in less exposed parts of the colony (Parrish 1995, Good 2002).

Numerous factors can potentially affect the size and reproductive success of seabird colonies, and the relative influence of these factors can differ among seabird colonies (e.g., Siegel-Causey and Hunt 1981, Léger and McNeil 1987), and perhaps among sub-colonies. The Double-crested Cormorant colony at East Sand Island first formed on the elevated rock breakwater at the western end of the island. As the size of the colony increased, it expanded eastward along the top of the breakwater, and nests continued to be built amongst the rocks. Recently, the colony on the breakwater fragmented and a portion of the colony began nesting in satellite sub-colonies on the lower ground near the rock breakwater.

Here we present findings from our investigations of factors limiting colony size and reproductive success at the largest colony of Double-crested Cormorants on the Pacific Coast of North America. Our objectives were to: (1) determine recent trends in colony size and reproductive success on East Sand Island, (2) examine commonly cited factors affecting productivity of seabird colonies to identify the most important constraints on reproductive success on East Sand Island, and (3) compare reproductive success between the main colony and recently formed sub-colonies to determine prospects for further expansion in colony size. We hypothesized that after the rapid expansion of the

cormorant colony on East Sand Island in the early to mid-1990s, colony growth has stabilized due to density-dependent effects on the availability of both food and nest sites. These constraints would be reflected in lower reproductive success, especially in recently formed satellite sub-colonies off the rock breakwater.

Methods

Study Area

East Sand Island (46°15'45"N, 123°57'45"W) is a 21-ha, naturally formed island that lies 6-8 river km inland from the Pacific Ocean in the Columbia River estuary, Clatsop County, Oregon (Figure 1.1). East Sand Island is owned and maintained by the U.S. Army Corps of Engineers and public access is not permitted on the island; however, fishing vessels and recreational boaters frequent the surrounding waters during the cormorant nesting season.

Double-crested Cormorants nest at the extreme western end of East Sand Island, entirely on the ground in nests made primarily from driftwood sticks gathered off-colony. The cormorants share East Sand Island with a large colony of Glaucous-winged/Western Gulls (*Larus glaucescens* X *L. occidentalis*) (ca. 6,000 pairs; D. Roby, unpubl. data), some of which nest in close proximity to the cormorant colony. These gulls are considered to be the main predators of Double-crested Cormorant eggs and nestlings, although other predators, such as Bald Eagles and

Peregrine Falcons (*Falco peregrinus*), may be significant sources of disturbance to the cormorant colony and thus enhance gull depredation on cormorant eggs and chicks.

Until recently, the East Sand Island cormorant colony was comprised of two substantial groups of nests that were built on an elevated rock breakwater used to stabilize the extreme western end of the island (Peters et al. 1978, see Figure 1.2). In 2000, the cormorant colony became more fragmented and, for the first time, discrete sub-colonies formed off the rock breakwater (dense groups of cormorant nests separated from the breakwater by >10 m). Sub-colonies comprised of 100's to 1000's of nests were found on both the breakwater (main colonies) and on the lower ground north of the breakwater (satellite colonies). Nests in the satellite colonies were built amongst driftwood hummocks and grassy vegetation, otherwise used by nesting gulls. In 2001, there were eight separate sub-colonies on the western end of East Sand Island. We focused our study on two sub-colonies, 1 located on the rock breakwater and part of the main colony, and 1 satellite sub-colony which was located on the lower ground in close proximity to the main sub-colony (~20 m; Figure 1.2).

Fig.1.1

fig. 1.2

Colony size

Numbers of Double-crested Cormorants nesting on East Sand Island have been estimated since 1991 by direct counts from aerial photographs taken during late incubation, when maximum colony attendance was assumed (Gaston and Smith 1984). Detailed methodology for aerial photography since 1997 is described in Collis et al. (2002). Briefly, individual adult cormorants located within delineated nesting areas on the photographs were enumerated using Zeiss PHOCUS software. A correction factor to convert number of individuals to number of breeding pairs was derived by determining in sample plots (from blinds near the colony) the fraction of the total number of adult cormorants on the colony that were incubating at the time the photographs were taken. The number of nesting pairs (colony size) was estimated by applying the correction factor to the direct count of adult cormorants on the colony. No estimates of colony size were made in 1990, 1992, or 1994.

Reproductive success

We collected data on reproductive success and nesting behaviour of Double-crested Cormorants from observation blinds during the 2001 nesting season. Blinds were elevated at least 1.5 m above the ground, equipped with one-way glass, and located on the periphery of the cormorant colony. Blinds were constructed in early April, before most cormorants arrived at the colony, and were suitably located to provide

unobstructed views of the two sub-colonies described above (Figure 1.2). Each blind was accessed through an above-ground, fabric-covered tunnel system that was entered at the north beach in order to minimize disturbance to the cormorant colony (Shugart et al. 1981, Figure 1.2).

We monitored a total of 142 active nests (nests containing at least 1 egg) to estimate productivity (young fledged/nesting pair) in the main sub-colony ($N = 81$ nests) and the satellite sub-colony ($N = 61$ nests) during 2001. Our sample of monitored nests included every nest within each of the sub-colonies where nest contents were visible from the observations blinds. A visual determination of the number of eggs and chicks per monitored nest was made each week from egg-laying to fledging (April 26 - July 24). Cormorant nests were viewed from blinds with the aid of binoculars and spotting telescopes. Nest initiation date was determined by the presence of a freshly-laid egg. If more than one egg was present in a nest on the first day when eggs were observed, nest initiation date was back-calculated by subtracting 1 d for each egg in the nest, (inter-egg interval is usually 1 d; Lewis 1929, Mitchell 1977, pers. obs.). When the visibility of eggs in the nest was poor, nest initiation date was estimated by subtracting the average incubation period (28 d; van Tets 1959, Mitchell 1977, Campbell 1990) from the hatching date. Because cormorant nestlings may leave ground nests as early as 21 d post-hatch (Hatch and Weseloh 1999), productivity (defined as the

number of young fledged per initiated nest) was estimated as the number of nestlings in each monitored nest at 20-25 d post-hatch.

We attempted to measure three nest site characteristics for each nest that was monitored during the 2001 nesting season. The vicinity of the East Sand Island cormorant colony is used as a post-breeding roost site by 1000's of endangered California Brown Pelicans (*Pelecanus occidentalis californicus*). To avoid disturbing pelicans, we waited until after they had vacated the roost in late November to measure cormorant nest site characteristics. By that time 15 monitored nests (12%) were no longer discernable on the colony. For each of the remaining 125 nests, we measured (± 1 cm) distance to the nearest neighbouring nest and distance to the edge of the sub-colony that abutted gull nesting habitat (herein referred to as "gull habitat") using a 25-m measuring tape. We measured nest elevation (± 0.5 in) relative to the lowest nest in the sample using a surveying level and leveling rod, and converted to cm.

Colony disturbances

We conducted 352 hours of behavioural observations between dawn and dusk from May 2 to July 25, 2001. Observation bouts lasted between 1 and 16 h (6.17 h ± 0.47 SE) and occurred on 57 different days (16-23 d/month). Start times for observation bouts were not randomly selected; instead, they occurred opportunistically throughout the season when access to the observation blinds was possible with minimal

disturbance to roosting California Brown Pelicans. We made observations from the blind located farthest west in the colony, which afforded simultaneous views of both sub-colonies under study (Figure 1.2).

We recorded all disturbances that noticeably affected behaviour of cormorants nesting in one or both of the two monitored sub-colonies, as well as the cause of the disturbance (when discernable) and the reaction of the sub-colony to the disturbance. Sub-colony reactions were graded by intensity, ranging from no visible response to flight response by the majority of or all nesting adults. For the purpose of this study, we defined a disturbance as an event that caused any nesting cormorant(s), in one or both of the monitored sub-colonies, to display visible signs of attention to an external stimulus. In some cases, cormorants nesting in one sub-colony were visibly disturbed while cormorants nesting in the other sub-colony did not show signs of disturbance. We classified the intensity of cormorant reactions as: (1) no response, the adult cormorants showed no apparent signs of disturbance; (2) alert response, adults lifted their heads, looked attentive, stood up from their nests; (3) alarm response, adults flapped their wings, leaned forward, walked around their nests in an agitated manner; (4) flight response, the majority of adults vacated the sub-colony. When a flight response occurred, the adult cormorants usually either circled above the colony before landing back on their nests or they landed on the water along the southern shore of the island and rafted there until the disturbance subsided.

Data Analysis

We used a weighted linear regression model (Ramsey and Schafer 1997) to investigate the trend in colony size estimates across years from 1989 to 2002 and tested the slope for significant difference from zero. Weights were $1/(SE)^2$; estimates with smaller standard errors received more weight. We calculated annual growth rates (λ) between years as: $\lambda = N_t/N_{t-1}$ (*sensu* Ricklefs 1979), using estimated number of nesting pairs from 1989 to 2002. When time between counts was 2 years, however, annual growth rates were calculated as: $\lambda = (N_t/N_{t-1})^{1/2}$.

We simulated the fecundity necessary to achieve the observed population growth rate for the period from 1991 to 2002 with a deterministic Leslie matrix model (S-PLUS 1999, Caswell 2001). Because there was unquestionably a major immigration event between 1989 and 1991 (see Results), we assumed the colony was established with 2026 breeding pairs in 1991 (Carter et al. 1995). We estimated population growth rate based on linear regression, using log-transformed estimates of number of nesting pairs. The Leslie matrix model was based on a pre-breeding census and 3 age classes with the following estimated annual survival rates: first-year survival (fledging to 1 year) of 0.48, second-year survival of 0.74, and subsequent annual survival of 0.85 (Van der Veen 1973). We assumed annual breeding probability to be 0%, 16.5%, and 78.8% for first, second, and >2 year age classes, respectively, as reported by Van der Veen (1973). We simulated a range of average annual

productivities (young fledged/nesting pair) necessary to achieve the estimated colony growth rate.

We investigated recent trends in productivity of the cormorant colony at East Sand Island from estimates that were made using methods consistent with those used in 2001. We used a one-way analysis of variance (ANOVA) F -test (Ramsey and Schafer 1997, S-PLUS 1999) to detect differences in annual productivity among the years 1997 to 2001. No comparable estimates of productivity were available from 1999. We used linear regression, weighted by $1/(SE)^2$, to examine trends in estimates of colony productivity over this 5-year period and we tested the significance of the slope. We used Wilcoxon rank-sum tests and Fisher's exact tests to determine if there were statistical differences in reproductive success between the main and satellite sub-colonies (Ramsey and Schafer 1997, S-PLUS 1999).

We used a Generalized Linear Model (Ramsey and Schafer 1997, SAS 1999) to examine factors influencing cormorant productivity during the 2001 nesting season. We fit a Poisson log-linear regression to our data to explore how Double-crested Cormorant productivity in 2001 was influenced by the categorical variable of nest site location (sub-colony) and the continuous variables of nest initiation date, nearest neighbour distance, distance to gull habitat, and nest elevation. We fixed the scale parameter at a value of one in the estimation procedure in order to account for potential under or over-dispersion. Additionally, we

considered a quadratic transformation of nest initiation data to account for potentially higher reproductive success of nests initiated during the peak of laying, compared to nests initiated earlier or later. We also considered the interaction terms of sub-colony*nearest neighbour distance, sub-colony*distance to gull habitat, and sub-colony*nest elevation; we used a likelihood ratio statistic to test for significance of effects.

We used a one-way ANOVA *F*-test to investigate potential differences in frequency of observed disturbances among the three months when we monitored the two sub-colonies in 2001. To further explore potential differences, we used *G*-tests for goodness-of-fit (Zar 1984) to determine whether the frequency of disturbance differed among causes of disturbance. *G*-tests were also used to determine whether intensity of sub-colony reactions differed by cause of disturbance or by month of the nesting season. We used a Generalized Linear Model with multinomial distribution for ordinal data (McCullagh and Nelder 1989, SAS 1999) to determine whether the distribution of reaction intensities to disturbances differed between cormorants nesting in the main sub-colony vs. the satellite sub-colony; we used a likelihood ratio statistic to test for significance of the effect. For all tests of significance, we used an alpha-level of 0.05 and reported two-tailed *P*-values.

Results

Colony size

The nesting colony of Double-crested Cormorants on East Sand Island has increased nearly 100-fold since the nesting colony was first recorded in 1989; in 2002 the colony consisted of an estimated 8,684 nesting pairs (Figure 1.3). The colony has consistently shown positive annual growth increments (Table 1.1). Over the past 11 years (1991-2002), the average annual population growth rate (λ) was 1.15 (linear regression model on log-transformed estimates: $F_{1,7} = 340$, $R^2 = 0.9798$, $P < 0.0001$).

Results from the Leslie matrix model indicated that the annual productivity of the colony would have needed to be 3.12 fledgings/nesting pair over the period 1991 to 2002 in order to yield the observed population growth rate, assuming no immigration. This fledging rate exceeds the maximum estimates of productivity for both the East Sand Island colony (2.02 ± 0.10 ; Figure 1.4) and from published studies of other Double-crested Cormorant colonies (2.59 ± 1.27 ; McNeil and Léger 1987, Hatch and Weseloh 1999). Therefore, it is probable that recruitment from other colonies, either within or outside of Oregon, continued to occur at the East Sand Island colony after 1991.

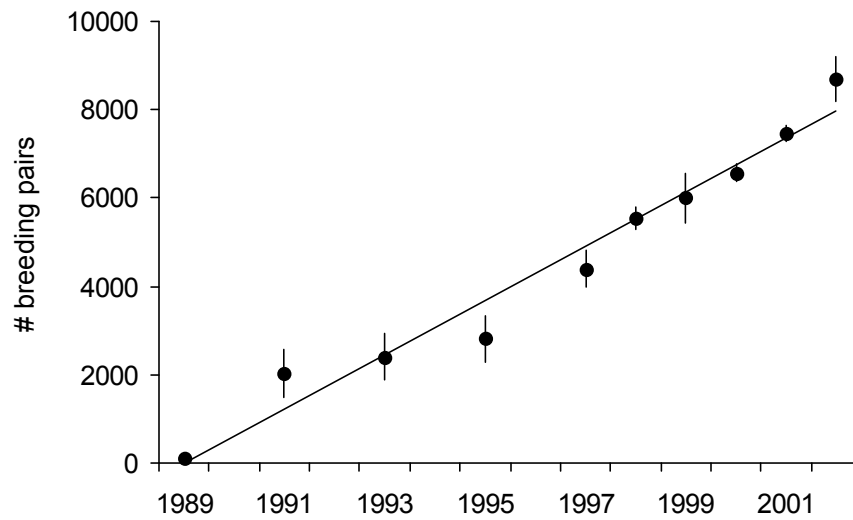


Figure 1.3. Estimated number of pairs (\pm SE) of Double-crested Cormorants nesting on East Sand Island, 1989-2001. (Linear regression: $F_{1,8} = 3062$, $r^2 = 0.997$, $P < 0.0001$).

Table 1.1. Estimated annual population growth rate (λ) of the nesting colony of Double-crested Cormorants at East Sand Island, 1989-2002.

Year	Annual population growth rate (λ)
1989 ¹	
1991 ²	4.72
1993 ³	1.09
1995 ³	1.08
1997 ⁴	1.25
1998 ⁴	1.26
1999 ⁴	1.08
2000 ⁴	1.09
2001 ⁴	1.14
2002 ⁴	1.16

¹ R. Lowe, USFWS, pers. comm.

² Carter et al. 1995

³ A. Clark, USFWS, pers. comm.

⁴ this study

Reproductive success

There were significant differences in estimates of annual productivity at East Sand Island among the four years when comparable estimates were available ($F_{3,299} = 102.85$, $P < 0.0001$), yet there was no clear linear trend in productivity during 1997 – 2001 ($F_{2,1} = 1.02$, $r^2 = 0.3368$, $P = 0.42$; Figure 1.4).

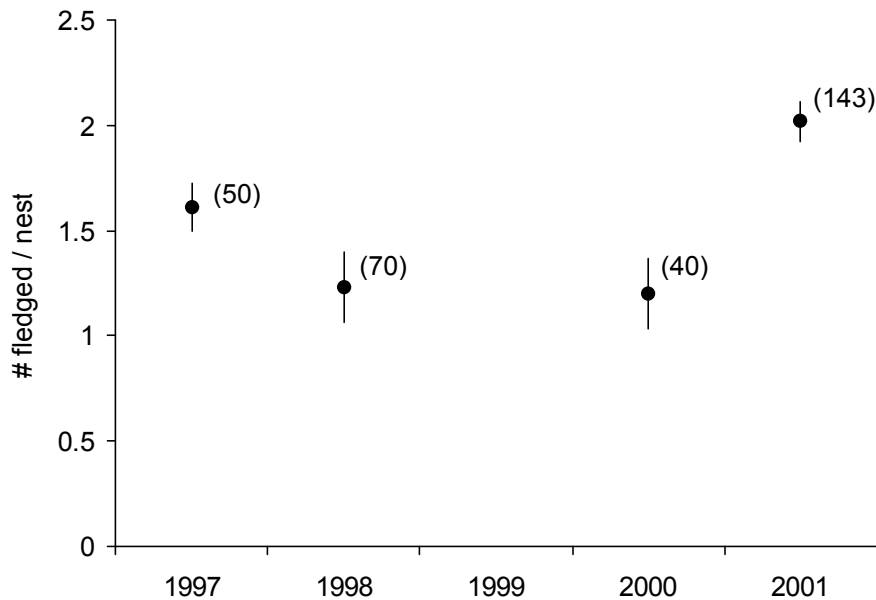


Figure 1.4. Estimated average productivity (young fledged/nesting pair) of Double-crested Cormorants nesting on East Sand Island, 1997-2001 (no estimate available for 1999). Numbers of nests monitored in each year are shown in parentheses.

Nests were first initiated in the main and satellite sub-colonies within two days of each other in 2001 (May 2 and May 4, respectively). However, cormorants nesting in the main sub-colony had a more protracted period of nest initiation; median nest initiation date for the main sub-colony was 11 d later than that for the satellite sub-colony (Wilcoxon rank-sum test: $Z = 2.554$, $N = 142$, $P = 0.011$; Table 1.2). Although clutch size ranged from 1-5 eggs in both sub-colonies, nests in the satellite sub-colony had significantly larger average clutch size and higher hatching success compared to nests in the main sub-colony (Wilcoxon rank-sum test: $Z = 4.462$, $N = 142$, $P < 0.0001$ and Fisher's exact test: $N = 142$, $P = 0.042$, respectively; Table 1.2).

Average productivity and average brood size at fledging were significantly greater in the satellite sub-colony than in the main sub-colony (Wilcoxon rank-sum test: $Z = 2.465$, $N = 142$, $P = 0.015$ and Wilcoxon rank-sum test: $Z = 2.018$, $N = 142$, $P = 0.044$, respectively; Table 1.2). Furthermore, nesting success in the satellite sub-colony averaged nearly 12% higher than in the main sub-colony (Fisher's exact test: $N = 142$, $P = 0.021$; Table 1.2). Nests in the satellite sub-colony were clearly more productive on average compared to nests in the main sub-colony.

There were distinct differences in colony shape between the main and satellite sub-colonies that may have contributed to differences in reproductive success. The main sub-colony was a long, narrow nesting area on the elevated rocky breakwater, whereas the satellite sub-colony

was more circular and on the lower ground adjacent to the breakwater
(see Figure 1.2).

Table 1.2. Reproductive success of Double-crested Cormorants nesting in main and satellite sub-colonies on East Sand Island in 2001. Averages are expressed as mean \pm SE.

	Main (<i>N</i> = 81 nests)	Satellite (<i>N</i> = 61 nests)	<i>P</i>
Median nest initiation date	May 19	May 10	0.011
Average clutch size	3.24 \pm 0.10	4.14 \pm 0.15	< 0.0001
Hatching success ¹	86.4%	96.7%	0.042
Brood size at fledging ²	2.18 \pm 0.10	2.52 \pm 0.12	0.044
Productivity ³	1.78 \pm 0.12	2.34 \pm 0.14	0.015
Nesting success ⁴	81.5%	93.4%	0.021

¹ Proportion of active nests hatching at least one egg

² Average number of young fledged (nestlings at 20-25 d post-hatch) per productive nest

³ Average number of young fledged per active nest

⁴ Proportion of active nests fledging at least one young

Although the perimeters of the main and satellite sub-colonies were similar (630.5 m and 560.4 m, respectively), the area of the satellite sub-colony (0.96 ha) was more than three times greater than that of the main sub-colony (0.30 ha). The main and satellite sub-colonies did not differ in nest density (0.10 and 0.12 nests/m², respectively).

After controlling for differences in various nest site characteristics (i.e., initiation date, nearest neighbour distance, elevation, distance from gull habitat), productivity was still 58% lower in the main sub-colony compared to the satellite sub-colony (Table 1.3). Combining nests from both sub-colonies, productivity was positively correlated with distance from gull habitat. There was a 13% (95% c.i. = 2% - 23%) increase in productivity with each 1 m increase in distance from gull habitat (Table 1.3). In contrast, there was no significant effect of nearest neighbour distance, nest elevation, and nest initiation date on productivity (Table 1.3). Nests initiated near the peak of laying were not more productive than nests initiated comparatively early or late during the laying period ($\chi^2_1 = 0.34$, $P = 0.561$). A drop-in-deviance F -test showed no evidence that the interaction terms or the quadratic transformation of the nest initiation date term improved the model ($t_{4,115} = 1.007$, $P > 0.25$); therefore, only the results from the reduced model are reported.

Table 1.3

Colony disturbances

We observed 166 disturbance events to the Double-crested Cormorants nesting in the main and satellite sub-colonies during 352 hours of behavioural observations (Table 1.4). Bald Eagles were the most common single cause of observed disturbances (43% or 72 events, Figure 1.5). Twenty-two percent of observed disturbances were attributed to anthropogenic causes, primarily anglers and recreational boaters ($N = 37$ events, Figure 1.5). The remaining 34% of observed disturbances could not be attributed to a particular cause ($N = 57$ events, Figure 1.5). Disturbances of unknown cause likely originated from inconspicuous, non-anthropogenic factors, such as raptors or small mammals. Nutria (*Myocastor coypus*) are numerous on the island, but difficult to detect as the cause of a disturbance.

The majority (70%) of observed disturbances to the East Sand Island cormorant colony occurred in May (Table 1.4), and this difference was significant ($F_{2,54} = 4.82$, $P = 0.01$). When causes of disturbances were considered separately, the frequency of Bald Eagle disturbances and unknown disturbances differed among the three months of the nesting season ($G_2 = 116.73$, $P < 0.001$ and $G_2 = 21.15$, $P < 0.001$, respectively); 88% of Bald Eagle disturbances ($N = 63$) and 63% of unknown disturbances ($N = 36$) occurred in May (Figure 1.5). The frequency of anthropogenic disturbances, however, did not differ among months of the nesting season ($G_2 = 1.78$, $P > 0.05$).

Table 1.4. Observed disturbance events at the East Sand Island Double-crested Cormorant colony in 2001. Averages are expressed as mean \pm SE. A disturbance event was defined as any event that caused the majority of nesting adults, in one or both of the monitored sub-colonies, to display visible signs of attention to an external stimulus.

Month	Number of observation days	% of observation days with disturbances	Number of observed disturbances	Frequency of disturbances (hr ⁻¹)
May	23	65.2	114	0.91 \pm 0.29
June	18	61.1	32	0.19 \pm 0.06
July	16	56.3	20	0.15 \pm 0.05
Season	57	61.4	166	0.47 \pm 0.13

In addition to frequency of disturbances, we considered the intensity of reactions by breeding adult cormorants in both the main and satellite sub-colonies. There was no difference in reaction intensity between the two sub-colonies to disturbances caused by human activity and unknown causes ($F_{188} = 0.21$, $P = 0.647$). The reaction intensity to Bald Eagle disturbances, however, differed between the two sub-colonies ($F_{144} = 9.20$, $P = 0.002$; Figure 1.6). During disturbances caused by eagles, cormorants nesting in the main sub-colony left their nests 70%

more frequently than cormorants nesting in the satellite sub-colony (34% and 20% of Bald Eagle disturbances, respectively; Figure 1.6).

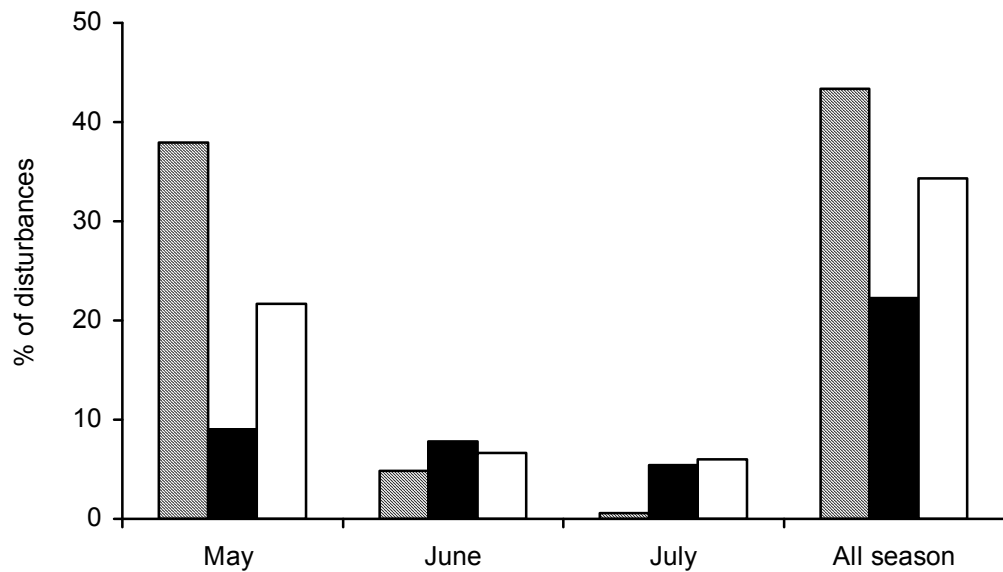


Figure 1.5. Percent of total disturbance events ($N = 166$) caused by Bald Eagles (gray bars), human activity (black bars), and unknown causes (white bars) observed for Double-crested Cormorants nesting at East Sand Island in 2001.

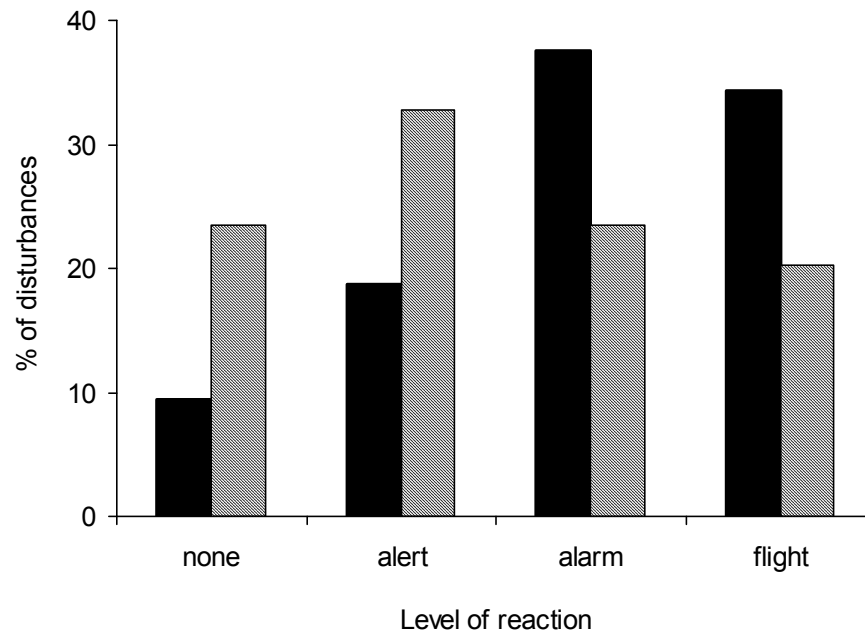


Figure 1.6. Intensity of reactions exhibited by nesting Double-crested Cormorants in response to Bald Eagle disturbances (N = 72) at a main sub-colony (black bars) and at a satellite sub-colony (gray bars) on East Sand Island in 2001. (Multinomial distribution for ordinal data: $\chi^2_1 = 9.20$, $P = 0.0024$).

Discussion

Food availability

Immigration has evidently played a key role in the dramatic increases in numbers of Double-crested Cormorants nesting at the East Sand Island colony. The recruitment of breeding adults likely reflects emigration from colonies in interior Oregon during drought years (Carter et al. 1995) and from coastal colonies in Washington, and perhaps British

Columbia, during years of poor ocean productivity (Wilson 1991). We speculate that food resources are more stable and predictable in the Columbia River estuary compared to coastal and interior nesting areas that are likely influenced to a greater extent by fluctuating oceanic and climatic conditions. Predictable food resources in the vicinity of East Sand Island likely makes the island an appealing nesting area to prospecting adult Double-crested Cormorants.

There is little evidence that intraspecific competition for food resources near the colony is regulating reproductive performance of Double-crested Cormorants in a density-dependent manner (cf. Ashmole 1963, Furness and Birkhead 1984). In 2001, the colony exhibited high productivity, suggesting that food resources were not limiting. Marine forage fish were comparatively abundant in the Columbia River estuary and plume in 2001 (Brodeur et al. in review, R. Emmett, NMFS, unpubl. data.). During years of low forage fish availability (i.e., El Niño years), however, reproductive success at the large cormorant colony on East Sand Island may become food-limited due to local depletion of prey resources near the colony.

Previous studies of other expanding colonies of Double-crested Cormorants suggested that colonies achieve high reproductive output (>2.2 young fledged/active nest) when the availability of prey resources is high, and then gradually decline as prey resources are depleted (e.g., Craven and Lev 1987, Hobson et al. 1989, Weseloh and Ewins 1994).

Lower food availability may lead to significant declines in reproductive performance of colonial seabirds, including reductions in clutch size, productivity, fledging weight, and fledgling survival (Gaston et al. 1983, Hunt et al. 1986, Birkhead and Furness 1985). Declines in reproductive performance may result in reduced recruitment to the colony and, consequently, limit colony size. During our study, there was no evidence that the East Sand Island cormorant colony was experiencing density-dependent effects on its size or productivity through food supply.

Nest site availability

Limitations on colony size due to availability of nest sites is considered unusual for seabird colonies (Birkhead and Furness 1985); however, there may be limited *quality* nest sites available to seabirds, even if potential nests sites remain unoccupied (e.g., Potts et al. 1980). There was strong evidence of a difference in reproductive success between sub-colonies at the East Sand Island cormorant colony. Surprisingly, nests located in a recently-established satellite sub-colony were more productive than nests located in the main sub-colony. Thus, Double-crested Cormorants nesting on East Sand Island in 2001 apparently used only a small proportion of the potentially available nesting habitat.

Several factors may make satellite sub-colonies attractive to prospecting male cormorants that arrive at the colony early in the breeding

season. First, nests in satellite sub-colonies may be more likely to persist from year to year as they are more protected than nests in the main sub-colony from wind and wave action during winter storms. Previous studies have shown that old nests in fairly good condition are preferred nest sites for returning cormorants (Mitchell 1977, Léger and McNeil 1987). Siegel-Causey and Hunt (1986) found that the probability of chick survival was higher at nest sites where nest structures persisted between years.

Second, prospecting cormorants that have observed productive conspecifics in previous years may attempt to recruit to the same nesting areas or may select nest site characteristics similar to those of successful cormorants (Boulinier and Danchin 1997, Danchin and Wagner 1997, Danchin et al. 1998, Schjorring et al. 1999).

Nest productivity at the East Sand Island cormorant colony was significantly and positively correlated with distance from gull habitat, regardless of sub-colony. Centrally located nest sites are generally chosen first by prospecting males that arrive at the colony early (Coulson 1968, Andrews and Day 1999). Central nests are often occupied by older and more experienced breeders (Siegel-Causey and Hunt 1986), which tend to lay more eggs and raise more chicks (DesGrange and Reed 1981). Our findings suggest that nest site location had a considerable influence on reproductive success at the East Sand Island colony. Contrary to our hypothesis, however, the satellite sub-colony was more productive than the main sub-colony.

A study conducted at Little Galloo Island, NY, previously the largest nesting colony of Double-crested Cormorants on the Great Lakes, reported that as the colony increased there was a dramatic increase in number of sub-colonies located in the interior of the island, separate from the original main colony area around the periphery of the island (Weseloh and Ewins 1994). On East Sand Island, considerable space still remains for expansion of the present satellite sub-colonies and/or establishment of new satellite sub-colonies. Because the satellite sub-colonies are experiencing high productivity, quality nesting habitat does not appear to be limiting. We expect that the East Sand Island cormorant colony will continue to expand into available nesting habitat during years of high forage fish availability.

Nest predation

The recent fragmentation of the previously continuous cormorant colony on East Sand Island created more “edge”, potentially resulting in more opportunities for gull predation on nest contents. The positive correlation between nest productivity and distance from gull habitat supports the hypothesis that the fragmented colony is less productive than a contiguous one. However, the productivity of pairs nesting in the satellite sub-colony was higher despite smaller average distance from gull habitat. A possible explanation is that, although the perimeter and nest density of the two sub-colonies under study were similar, the satellite sub-

colony covered a greater area and was circular in shape. Therefore, more pairs nesting in the satellite sub-colony were surrounded by neighbours, affording more protection from gull attacks on nest contents, compared to the long and narrow main sub-colony. Also, the satellite sub-colony was established amongst driftwood hummocks and grassy vegetation that is easily traversed by cormorants, unlike the large rock rubble and driftwood logs that form the elevated breakwater where the main sub-colony was situated. On several occasions, we observed cormorants in the satellite sub-colony mounting a group defense to protect their nests from gulls, a defense strategy reported in other studies of nesting Double-crested Cormorants (e.g., Kury and Gochfeld 1975). We speculate that this group defense behaviour may have been a reflection of the enhanced mobility of cormorants nesting in the satellite sub-colony.

It is well-documented that cormorants will aggressively defend their nests against marauding gulls (Kury and Gochfeld 1975, Siegel-Causey and Hunt 1981, Verbeek 1982). In most cases, however, gulls are not efficient nest predators in the absence of a source of disturbance to nesting adult cormorants. While Bald Eagles infrequently prey on adult cormorants (we observed only one attempted predation event) or their eggs and nestlings, eagles are the primary source of disturbance to nesting cormorants on East Sand Island. Although cormorants and their young have been reported as eagle prey (Campbell 1969, Todd et al. 1982, Watson et al. 1991, Jackman et al. 1999), studies of Bald Eagle

food habits in the Columbia River estuary indicate that eagles feed primarily on fish (90% of food items; Watson et al. 1991).

Bald Eagles caused considerable indirect effects on the productivity of the Double-crested Cormorant nesting colony at East Sand Island. As Wootton (1994) stated, “indirect effects occur when the impact of one species on another requires the presence of a third species”. At East Sand Island, eagle disturbances frequently caused cormorants to fly off their nests, leaving eggs and nestlings vulnerable to depredation by predators, primarily gulls. In 2001, cormorants reacted more often and more intensely to Bald Eagle disturbances than to any other type of disturbance. Moreover, the frequency of Bald Eagle disturbances was higher early in the nesting season, when nests contained eggs.

There are two apparent reasons for higher rates of eagle disturbance in May. First, cormorants at the East Sand Island colony are nest-building, egg-laying, and incubating during May. Previous studies have shown that seabirds with less investment in reproduction early in the season are more likely to respond to perceived threats and thereby avoid risk to themselves (Siegel-Causey and Hunt 1981, Parrish 1995). As the nesting season advances and reproductive investment increases, breeding adult cormorants become more tolerant of disturbances (Kury and Gochfeld 1975). Second, Bald Eagles occur in greater numbers (both nesting adults and immatures) between February and May in the Columbia River estuary (Isaacs et al. 1983, Jenkins et al. 1999). Eagle

disturbance events at the cormorant colony were primarily caused by immature eagles, although adult eagles also contributed. This is likely a reflection of the high ratio of immatures to adult eagles (3:1) reported in the Columbia River estuary during peak abundance (Garrett et al. 1988). In June, immature eagles typically migrate north from winter and spring foraging areas and become less numerous in the Columbia River estuary (Broley 1947, Hunt et al. 1992, Jenkins et al. 1999; F. Isaacs, Oregon Cooperative Fish and Wildlife Research Unit, pers. comm.).

There are two possible explanations for the greater frequency and intensity of reactions to Bald Eagles by cormorants nesting in the main sub-colony. First, the average potential reproductive output of cormorants nesting in the main sub-colony was less than the satellite sub-colony (i.e., smaller average clutch size and brood size), perhaps resulting in more intense reactions to perceived threats. Second, more intense reactions by cormorants nesting in the main sub-colony may be related to eagle foraging behaviour. Eagles were commonly seen flying along the southern shore of the island (over the main sub-colony) and were frequently observed perching on driftwood logs and stumps that are strewn along the breakwater at the western end of the main colony. It is likely that eagles were searching the southern shoreline for fish carcasses that washed ashore; studies of Bald Eagles in the Columbia River estuary found that eagles feed primarily on fish scavenged from shorelines, exposed beaches, and tidal islands at low-tide (McGarigal et al. 1991).

Numbers of Bald Eagles residing in the Columbia River estuary have increased dramatically over the last decade (Isaacs and Anthony 2002), like numbers of Double-crested Cormorants. Double-crested Cormorants and Bald Eagles are both native to the region and it is likely that eagles play a role in maintaining healthy cormorant populations. It is known, however, that nest predation by gulls and crows, aided by colony disturbances caused by Bald Eagles, can have devastating effects on reproductive success of open-nesting, coastal seabirds in the Pacific Northwest (Verbeek 1982, Parrish et al. 2001, Moul and Gebauer 2002). Some large nesting colonies of Double-crested Cormorants in British Columbia have suffered near complete reproductive failure and abandonment due to increased levels of Bald Eagle activity (Moul and Gebauer 2002). It is well-documented that cormorants exhibit plasticity in nest site selection, and will shift among colonies in response to changing food availability (Hodder and Graybill 1985, Bayer 1986, Wilson 1991), nesting habitat (Weseloh and Ewins 1994, Van Eerden and Gregersen 1995), and level of disturbance (Henny 1989, Cairns et al. 1998).

Reduced availability of marine forage fish due to El Niño events or regime shifts may exacerbate the effects of Bald Eagle disturbance on reproductive success of Double-crested Cormorants at East Sand Island. First, eagles may spend more time searching shorelines and perching at foraging areas located within or in close proximity to the cormorant colony, causing more disturbance to nesting cormorants. Second, eagles may

increase depredation rates on cormorant adults, nest contents, and fledglings when fish prey are less abundant. Third, common nest predators (i.e., gulls) may become more aggressive and persistent in depredating cormorant eggs and nestlings, and pirating cormorant regurgitations, as other food resources become less abundant. Finally, lower forage fish availability will likely reduce the reproductive potential and commitment of nesting cormorants, making it easier for gulls and other nest predators to depredate eggs and chicks. For these reasons, we believe that depredation by gulls following eagle disturbances may be the primary factor limiting the reproductive success and, ultimately, the size of the Double-crested Cormorant colony on East Sand Island, especially if the availability of forage fishes declines.

Management implications

There is considerable overlap in the breeding and wintering areas of the West Coast subspecies of Double-crested Cormorants (Hatch and Weseloh 1999). Double-crested Cormorants banded as nestlings in British Columbia have been resighted in Oregon (Moul 1996) and adults tagged at East Sand Island have been relocated throughout Puget Sound, the Straits of Juan de Fuca, and into British Columbia. These resightings support the hypothesis that Double-crested Cormorants nesting at colonies throughout the Pacific Northwest belong to one population. The extent of exchange with colonies further south in California and Baja

California is less certain. Regardless of population boundaries, the nesting colony of Double-crested Cormorants at East Sand Island represents a substantial proportion of the numbers of *P. a. albociliatus* breeding in the Pacific Northwest and throughout the west coast from British Columbia to Sinaloa, Mexico.

The numbers of Double-crested Cormorants on the Pacific Coast of North America were recently estimated at 17,100 nesting pairs. This estimate included both the West Coast subspecies (*albociliatus*) and the Alaskan subspecies (*cincinatus*; $N = 2,935$ nesting pairs; Tyson et al. 1999). Based on the most recent regional population data available, we conservatively estimated that the Double-crested Cormorant colony on East Sand Island represented >40% of *P. a. albociliatus* breeding adults. To arrive at this estimate, we made the following adjustments to the most recent estimate of species along the Pacific Coast (Tyson et al. 1999). First, we excluded the Alaskan subspecies, which represented ca. 17% of the Pacific Coast numbers at the time the survey was conducted (B. Blackwell, United States Department of Agriculture, pers. comm.). Second, we added 6,660 nesting pairs to the estimate of the total population size to account for the large increase in size of the East Sand Island colony since 1992, when colony was counted for the Tyson et al. (1999) estimate. Finally, we assumed all other colonies have remained stable since the time of the most recent survey.

The East Sand Island colony may represent a greater proportion of the population of the West Coast subspecies for several reasons. First, colony sizes have not remained stable since 1992. Numerous West Coast colonies have experienced dramatic declines (100's to 1000's of nesting pairs) over the past decade since the surveys reported in Tyson et al. (1999) were conducted (e.g., Rice Island in the Columbia River estuary, OR; Mandarte Island and the Chain Islets in the Gulf Islands, BC; South Farallon Island, CA). Second, to our knowledge, very few West Coast colonies have increased in numbers of nesting pairs over the past decade. Exceptions include the East Sand Island colony and the Mullet Island colony in the Salton Sea, California. However, the Mullet Island colony was abandoned in 2001 (K. Molina, National History Museum of Los Angeles County, pers. comm.). Third, there have been few reports of new Double-crested Cormorant colonies along the west coast since Tyson et al. (1999). Six new Double-crested Cormorant nesting colonies have been discovered along the Oregon coast since 1992; however, it is likely that the new colonies were formed by cormorants emigrating from nearby nesting areas (R. Lowe, USFWS, pers. comm.).

There are few recent data available on productivity and demography of the West Coast subspecies of Double-crested Cormorant. In many cases, surveys conducted over a decade ago (see Carter et al. 1995) represent the only demographic data available for *P. a. albociliatus*. More recent and range-wide data are necessary to begin to understand

the extent to which factors limiting colony size and reproductive success at the East Sand Island colony are also influencing population trends of Double-crested Cormorants throughout the Pacific coast of North America. Despite dramatic increases in the size of the East Sand Island cormorant colony in the last 13 years, there is evidence that the numbers of *P. a. albociliatus* may be in decline. In light of this uncertainty, recent proposals to manage and control the breeding and wintering populations of Double-crested Cormorants throughout the contiguous U.S. (USFWS 2001) should be reconsidered on a region-by-region basis. We advocate that the subspecies *P. a. albociliatus* be considered a distinct population segment (USFWS 1988) and managed according to overall population size and trends for this subspecies.

Literature Cited

- Aebischer, N.J. 1986. Retrospective investigation of an ecological disaster in the Shag, *Phalacrocorax aristotelis*: A general method based on long-term marking. *Journal of Animal Ecology* 55:613-629.
- Ainley, D.G., and R.J. Boekelheide (eds.). 1990. *Seabirds of the Farallon Islands*. Stanford University Press, Stanford, CA. 450 pp.
- Anderson, D.J., and P.J. Hodum. 1993. Predator behavior favors clumped nesting in an oceanic seabird. *Ecology* 74:2462-2464.
- Andrews, D.J., and K.R. Day. 1999. Reproductive success in the Great Cormorant *Phalacrocorax carbo carbo* in relation to colony nest position and timing of nesting. *Atlantic Seabirds* 1:107-120.
- Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-473.
- Bayer, R. 1986. Breeding success of seabirds along the mid-Oregon coast concurrent with the 1983 El Niño. *Murrelet* 67:23-26.
- Birkhead, T.R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). *Journal of Animal Ecology* 46:751-764.
- Birkhead, T.R., and R.W. Furness. 1985. The regulation of seabird populations. Pages 145-167 in Sibly, R.M., and R.H. Smith (eds.), *Behavioural Ecology*. Blackwell, Oxford.
- Birt, V.L., T.P. Birt, D. Goulet, D.K. Cairns, and W.A. Montevecchi. 1987. Ashmole's halo: Direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40:205-208.
- Boulinier, T., and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology* 11:505-517.
- Brodeur, R., W.G. Pearcy, and S. Ralston. *In review*. Abundance and distribution patterns of nekton and micronekton in the Northern California current transition zone. *Journal of Oceanography*.
- Broley, C.L. 1947. Migration and nesting of Florida Bald Eagles. *Wilson Bulletin* 59:1-68.

- Brunton, D.H. 1977. Impacts of predators: Center nests are less successful than edge nests in a large nesting colony of Least Terns. *Condor* 99:372-380.
- Cairns, D.K. 1992. Population regulation of seabird colonies. Pages 37-61 *in* D.M. Power (ed.), *Current ornithology*. Vol. 9. Plenum, New York, NY.
- Cairns, D.K., R.L. Dibblee, and P.-Y. Daoust. 1998. Displacement of a large Double-crested Cormorant, *Phalacrocorax auritus*, colony following human disturbance. *Canadian Field-Naturalist* 112:520-522.
- Campbell, R.W. 1969. Bald Eagle swimming in ocean with prey. *Auk* 86:561.
- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. 1990. The birds of British Columbia. Vol.1. Nonpasserines: loons through waterfowl. Royal British Columbia Museum, Victoria, and Canadian Wildlife Service, Delta, BC. 535 pp.
- Cannings, R.J. 1998. The birds of British Columbia – a taxonomic catalogue. British Columbia Ministry of the Environment, Lands and Parks, Wildlife Branch, Victoria, BC. Wildlife Bulletin No. B-86. 252 pp.
- Carter, H.R., A.L. Sowls, M.S. Rodway, U.W. Wilson, R.W. Lowe, G.J. McChesney, F. Gress, and D.L. Anderson. 1995. Population size, trends, and conservation problems of the Double-crested Cormorant on the Pacific Coast of North America. *Colonial Waterbirds* 18 (Special Publication 1):189-215.
- Caswell, H. 2001. *Matrix population models: Construction, analysis and interpretation*, 2nd ed. Sinauer Assoc., Inc., Sunderland, MA. 722 pp.
- Clode, D. 1993. Colonially breeding seabirds: Predators or prey? *Trends in Ecology and Evolution* 8:336-338.
- Collis, K., D.D. Roby, D.P. Craig, S.L. Adamany, J.Y. Adkins, and D.E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537-550.

- Conservation Data Centre. 2002. RED and BLUE LISTS for British Columbia amphibians, reptiles, birds, and mammals. At <http://srmwww.gov.bc.ca/cdc/tracking.htm>.
- Coulson, J.C. 1968. Differences in the quality of birds nesting in the center and on the edge of a colony. *Nature* 217:211-227.
- Craven, S.R., and E. Lev. 1987. Double-crested Cormorants in the Apostle Islands, Wisconsin, USA: Population trends, food habits and fishery deprecations. *Colonial Waterbirds* 10:64-71.
- Danchin, E., and R.H. Wagner. 1997. The evolution of coloniality: The emergence of new perspectives. *Trends in Ecology and Evolution* 14:405-410.
- Danchin, E., T. Boulinier, and M. Massot. 1998. Breeding habitat selection based on conspecific reproductive success: Implications for the evolution of coloniality. *Ecology* 79:2415-2428.
- DesGranges, J.L., and A. Reed. 1981. Disturbance and control of selected colonies of Double-crested Cormorants in Quebec. *Colonial Waterbirds* 4:12-19.
- Emmett, R., and R. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. *North Pacific Anadromous Fish Commission Bulletin* 2:11-20.
- Furness, R.W. 1984. Influences of adult age and experience, nest location, clutch size and laying sequence on the breeding success of the Great Skua *Catharacta skua*. *Journal of Zoology (London)* 202:565-576.
- Furness, R.W., and T.R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655-656.
- Furness, R.W., and P. Monaghan. 1987. *Seabird ecology*. Blackie, Oxford. 164 pp.
- Garrett, M., R.G. Anthony, J.W. Watson, and K. McGarigal. 1988. Ecology of Bald Eagles on the lower Columbia River. Report to the United States Army Corps of Engineers, Portland, OR. 191 pp.

- Gaston, A.J., G. Chapdelaine, and D.G. Noble. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: Inter- and intra-colony variation. *Canadian Journal of Zoology* 61:2465-2475.
- Gaston, A.J., and G.E.J. Smith. 1984. The interpretation of aerial surveys for seabirds: Some effects of behaviour. *Canadian Wildlife Service Occasional Paper* 53:1-20.
- Good, T.P. 2002. Breeding success in the Western Gull X Glaucous-winged Gull complex: The influence of habitat and nest-site characteristics. *Condor* 104:353-365.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:142-159.
- Hatch, J.J. 1995. Changing populations of Double-crested Cormorants. *Colonial Waterbirds* 18 (Special Publication 1):8-24.
- Hatch, J.J., and D.V. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). In *The Birds of North America*, No. 441 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA. 36 pp.
- Hatchwell, B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*). *Journal of Animal Ecology* 60:721-736.
- Henny, C.J., L.J. Blus, S.P. Thompson, and U.W. Wilson. 1989. Environmental contaminants, human disturbance and nesting of Double-crested Cormorants in Northwestern Washington. *Colonial Waterbirds* 12:198-206.
- Hobson, K.A., R.W. Knapton, and W. Lysack. 1989. Population, diet and reproductive success of Double-crested Cormorants breeding on Lake Winnipegosis, Manitoba, in 1987. *Colonial Waterbirds* 12:191-197.
- Hodder, J., and M.R. Graybill. 1985. Reproduction and survival of seabirds in Oregon during the 1982-1983 El Niño. *Condor* 87:535-541.
- Hunt, G.L. Jr., Z.A. Eppley, and D.C. Schneider. 1986. Reproductive performance of seabirds: The importance of population and colony size. *Auk* 103:306-317.

- Hunt, W.G., R.E. Jackman, J.M. Jenkins, C.G. Thelander, and R.E. Lehman. 1992. Northward post-fledging migration of California Bald Eagles. *Journal of Raptor Research* 25:19-23.
- Isaacs, F.B., and R.G. Anthony. 2002. Bald Eagle nest locations and history of use in Oregon and the Washington portion of the Columbia River Recovery Zone, 1971 through 2001. Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR. 33 pp.
- Isaacs, F.B., R.G. Anthony, and R. J. Anderson. 1983. Distribution and productivity of nesting Bald Eagles in Oregon 1978-1982. *Murrelet* 64:33-38.
- Jackman, R.E., W.G. Hunt, J.M. Jenkins, and P.J. Detrich. 1999. Prey of nesting Bald Eagles in northern California. *Journal of Raptor Research* 33:87-96.
- Jenkins, J.M., R.E. Jackman, and W.G. Hunt. 1999. Survival and movements of immature Bald Eagles fledged in northern California. *Journal of Raptor Research* 33:81-86.
- Kruuk, H. 1964. Predators and antipredator behaviour of the Black-headed Gull (*Larus ridibundus*). *Behaviour, Supplement* 11:1-129.
- Kury, C.R., and M. Gochfeld. 1975. Human interference and gull predation in cormorant colonies. *Biological Conservation* 8:23-34.
- Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. *Proceedings of the International Ornithological Congress* 14:30-42.
- Léger, C., and R. McNeil. 1987. Choix de l'emplacement des nids de Cormorans à Aigrettes (*Phalacrocorax auritus*) aux îles de la Madeleine, Québec. *Canadian Journal of Zoology* 65:24-34.
- Lewis, H.F. 1929. The natural history of the Double-crested Cormorant (*Phalacrocorax auritus auritus* (Lesson)). Ru-Mi-Lou Books, Ottawa, ON. 94pp.
- McCullagh, P., and J.A. Nelder. 1989. *Generalized Linear Models*, 2nd ed. Chapman & Hall, London, UK. 511 pp.

- McGarigal, K., R.G. Anthony, and F.B. Isaacs. 1991. Interactions of humans and Bald Eagles on the Columbia River estuary. *Wildlife Monographs*, No.115. The Wildlife Society, Inc. 47 pp.
- McNeil, R., and C. Léger. 1987. Nest-quality and reproductive success of early- and late-nesting Double-crested Cormorants. *Wilson Bulletin* 99:262-267.
- Mitchell, R.M. 1977. Breeding biology of the Double-crested Cormorant on Utah Lake. *Great Basin Naturalist* 37:1-23.
- Moul, I.E. 1996. Seasonal movement patterns of Double-crested Cormorants in the Strait of Georgia and Puget Sound 1994-1996. Unpublished report. Canadian Wildlife Service, Pacific Wildlife Research Centre, Delta, BC. 111 pp.
- Moul, I.E. 2000. Population trends of Double-crested and Pelagic cormorants nesting along the southern coast of Vancouver Island, 1999. Unpublished report, British Columbia Ministry of the Environment, Lands and Parks, Nanaimo, BC. 21 pp.
- Moul, I.E., and M.B. Gebauer. 2002. Status of the Double-crested Cormorant in British Columbia. British Columbia Ministry of Water, Land, and Air Protection, Biodiversity Branch, Victoria, BC. *Wildlife Working Report No. WR-105*. 36 pp.
- Paine, R.T., J.T. Wootton, and P.D. Boersma. 1990. Direct and indirect effects of Peregrine Falcon predation on seabird abundance. *Auk* 107:1-9.
- Palacios, E., and E. Mellink. 2000. Nesting waterbirds on Isla San Martin and Todos Santos, Baja California. *Western Birds* 31:184-189.
- Parrish, J.K. 1995. Influence of group size and habitat type on reproductive success in Common Murres (*Uria aalge*). *Auk* 112:390-401.
- Parrish, J.K., M. Marvier, and R.T. Paine. 2001. Direct and indirect effects: Interactions between Bald Eagles and Common Murres. *Ecological Applications* 11:1858-1869.
- Peters, C.F., K.O. Richter, D.A. Manuwal, and S.G. Herman. 1978. Colonial nesting sea and wading bird use of estuarine islands in the Pacific Northwest, Technical Report D-78-17. Final Report by John Graham Company, Seattle, WA. 220 pp.

- Potts, G.R., J.C. Coulson, and I.R. Deans. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *Journal of Animal Ecology* 49:465-484.
- Ramsey, F.L., and D.W. Schafer. 1997. *The statistical sleuth: A course in methods of data analysis*. Wadsworth Publ. Co., Belmont, CA. 742 pp.
- Regehr, H.M., M.S. Rodway, and W.A. Montevecchi. 1998. Antipredator benefits of nest-site selection in Black-legged Kittiwakes. *Canadian Journal of Zoology* 76:910-915.
- Ricklefs, R.E. 1979. *Ecology*, 2nd ed. Chiron Press, Inc., New York, NY. 966 pp.
- Rodway, M.S. 1991. Status and conservation of breeding seabirds in British Columbia. Pages 43-102 in J.P. Croxall (ed.), *Seabird status and conservation: A supplement*. Technical Publication No. 11. International Council for Bird Preservation, Cambridge, UK.
- Rolland, C. E., E. Danchin, and M. de Fraipont. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: A comparative analysis. *American Naturalist* 151:514-529.
- Rowe, S., and I.L. Jones. 2000. The enigma of Razorbill *Alca torda* breeding site selection: Adaptation to a variable environment? *Ibis* 142:324-327.
- SAS Institute Inc. 1999. *SAS/STAT Software, Version 8*. SAS Institute Inc., Cary, NC.
- Sauer, J.R., J.E. Hines, G. Gough, I. Thomas, and B.G. Peterjohn. 1997. *The North American breeding bird survey results and analysis. Version 96.4*. Patuxent Wildlife Research Center, Laurel, MD. At www.mbr-pwrc.usgs.gov/bbs/.
- Schjorring, S., J. Gregersen, and T. Bregnballe. 1999. Prospecting enhances breeding success of first-time breeders in the Great Cormorant, *Phalacrocorax carbo sinensis*. *Animal Behaviour* 57:647-654.

- Shugart, G.W., M.A. Fitch, and V.M. Shugart. 1981. Minimizing investigator disturbance in observational studies of colonial waterbirds: Access to blinds through tunnels. *Wilson Bulletin* 93:565-569.
- Siegel-Causey, D., and G.L. Hunt. 1981. Colonial defense behavior in Double-crested and Pelagic cormorants. *Auk* 98:522-531.
- Siegel-Causey, D., and G.L. Hunt. 1986. Breeding-site selection and colony formation in Double-crested and Pelagic cormorants. *Auk* 103:230-234.
- Siegel-Causey, D., and S.P. Kharitonov. 1990. The evolution of coloniality. Pages 285-330 *in* D.M. Power (ed.), *Current ornithology*. Vol. 7. Plenum, New York, NY.
- Spear, L.B. 1993. Dynamic and effect of Western Gulls feeding in a subcolony of guillemots and Brandt's Cormorants. *Journal of Animal Ecology* 62:399-414.
- S-PLUS. 1999. S-plus 2000, Release 3. MathSoft, Inc., Seattle, WA.
- Todd, C.S., L.S. Young, R.B. Owen, and F.J. Gramlich. 1982. Food habits of Bald Eagles in Maine. *Journal of Wildlife Management* 46:636-645.
- Tyson, L.A., J.L. Belant, F.J. Cuthbert, and D.V. Weseloh. 1999. Nesting populations of Double-crested Cormorants in the United States and Canada. Pages 17-26 *in* M.E. Tobin (ed.), *Symposium on Double-crested Cormorants: Population status and management issues in the Mid-west*. USDA/APHIS Tech. Bull. No. 1879. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Washington, DC. 164 pp.
- USFWS (United States Fish and Wildlife Service). 1988. Endangered species act of 1973. As amended through the 100th Congress. U.S. Department of the Interior, Washington, D.C.
- USFWS (United States Fish and Wildlife Service). 2001. Draft environmental impact statement: Double-crested Cormorant management. United States Department of the Interior, Fish and Wildlife Service, Washington, DC. 152 pp.

- Van der Veen, H.E. 1973. Some aspects of the breeding biology and demography of the Double-crested Cormorants (*Phalacrocorax auritus*) of Mandarte Island. Ph.D. thesis, Zoologisch Laboratorium der Rijksuniversiteit te Groningen, Groningen *in* Hatch and Weseloh (1999).
- Van Eerden, M.R., and J. Gregersen. 1995. Long-term changes in the northwestern European population of cormorants. *Ardea* 83:61-79.
- van Tets, G.F. 1959. A comparative study of some social communication patterns in the Pelecaniformes. Ornithological Monograph No. 2: American Ornithologists' Union, Washington, DC.
- Verbeek, N.A.M. 1982. Egg predation by Northwestern Crows: Its association with human and Bald Eagle activity. *Auk* 99:347-352.
- Watson, J.W., M.G. Garrett, R.G. Anthony. 1991. Foraging ecology of Bald Eagles in the Columbia River estuary. *Journal of Wildlife Management* 55:492-499.
- Weseloh, D.V.C., and P.J. Ewins. 1994. Characteristics of a rapidly increasing colony of Double-crested Cormorants (*Phalacrocorax auritus*) in Lake Ontario: Population size, reproductive parameters and band recoveries. *Journal of Great Lakes Research* 20:443-456.
- Wilson, U.W. 1991. Responses of three seabird species to El Niño events and other warm episodes on the Washington coast, 1979-1990. *Condor* 93:853-858.
- Wires, L.R., F.J. Cuthbert, D.R. Trexel, and A.R. Joshi. 2001. Status of the Double-crested Cormorant (*Phalacrocorax auritus*) in North America. Final Report to United States Fish and Wildlife Service. University of Minnesota, St. Paul, MN. 360 pp.
- Wittenberger, J.F., and G.L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. Pages 1-78 *in* D.S. Farner, J.R. King, and K.C. Parkes (eds.), *Avian biology*. Vol. 8. Academic Press, Inc., New York, NY. 256 pp.
- Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443-466.
- Wright, H.W. 1913. The birds of San Martín Island, Lower California. *Condor* 15:207-210.

Zar, J.H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 pp.

CHAPTER 3

FORAGING PATTERNS OF MALE AND FEMALE
DOUBLE-CRESTED CORMORANTS
NESTING IN THE COLUMBIA RIVER ESTUARY

Cynthia D. Anderson, Daniel D. Roby, and Nathan D. Chelgren

Abstract

The nesting colony of Double-crested Cormorants (*Phalacrocorax auritus albociliatus*) on East Sand Island in the Columbia River estuary is currently the largest for this species on the Pacific Coast of North America. We used radio-telemetry to investigate the spatial and temporal foraging patterns of nesting cormorants to better understand how this colony of piscivores meets its resource needs, particularly with regard to use of out-migrating juvenile salmonids as a food source. We determined that nesting adults tended to forage >5 km from the colony and foraging distribution was distinctly different between the sexes. On average, males commuted nearly twice the distance to forage compared to females. Females typically foraged in the estuarine-mixing zone, reportedly the region of the estuary with the greatest densities of schooling fishes, while males tended to commute over 15 km to forage in the freshwater zone. Foraging intensity of both sexes varied by time of day, tide stage, and tide series; foraging generally intensified during ebb tides. These gender differences in foraging patterns, combined with the ability to forage at considerable distance from the colony on a wide variety of prey, may allow this large and growing colony to remain productive while competing for food with many thousands of other piscivorous waterbirds that use East Sand Island. Despite foraging patterns that seem conducive to high predation rates on juvenile salmonids, particularly for males, neither sex

relied on this prey type for more than a small fraction of its food requirements during the study.

Introduction

The nesting colony of Double-crested Cormorants (*Phalacrocorax auritus*) on East Sand Island near the mouth of the Columbia River is currently the largest for this species on the Pacific Coast of North America (Carter et al. 1995, Collis et al. 2002). In contrast to declines in numbers of Double-crested Cormorants nesting at other colonies along the coast of the Pacific Northwest, the East Sand Island colony has grown dramatically. The colony grew from less than 100 pairs (R. Lowe, USFWS, pers. comm.) to over 8,500 breeding pairs in the last 13 years, and now represents a substantial proportion (>40%) of the West Coast population (see Chapter 1). Because the nesting season of these piscivorous waterbirds coincides with peak out-migration of juvenile salmonids (*Oncorhynchus* spp.) from the Columbia River basin (FPC 2002), cormorant predation may be a significant source of mortality for migrating smolts, many of which are listed as either threatened or endangered under the U.S. Endangered Species Act (ESA; NMFS 2002).

The impacts of predation by Double-crested Cormorants on commercially important fish stocks have been studied extensively and there is little evidence to suggest that cormorants seriously deplete commercially-valued fish populations (reviews in Hatch and Weseloh

1999, Trapp et al. 1997). Cormorants may, however, be a significant source of fish mortality at sites where fish prey are aggregated (e.g., hatcheries or fish farms; Nettleship and Duffy 1995). Recent studies of Double-crested Cormorant diets in the Columbia River estuary revealed that juvenile salmonids were the most prevalent prey type for cormorants nesting on Rice Island in the upper estuary (river km 34), whereas the diet of cormorants nesting on East Sand Island (river km 7) included substantially fewer salmonids (one third as much by mass; Collis et al. 2002). Presumably, the major differences in diet composition between cormorant colonies reflect differences in foraging distribution within the estuary. Based on these diet differences and central place foraging theory (Maurer 1996), we hypothesized that cormorants nesting on islands in the Columbia River estuary were maximizing foraging efficiency by foraging in proximity to their nesting colonies.

The Double-crested Cormorants nesting on East Sand Island currently share the island with ca. 9,900 nesting pairs of Caspian Terns (*Sterna caspia*), ca. 6,000 nesting pairs of Glaucous-winged/Western Gulls (*Larus glaucescens* X *L. occidentalis*) (D. Roby, unpubl. data), as well as thousands of post-breeding California Brown Pelicans (*Pelecanus occidentalis*) (S. Wright, OSU, unpubl. data). The predation pressure associated with a large and growing colony of cormorants and other piscivores may lead to local forage fish depletion in the vicinity of East Sand Island (Ashmole 1963, Furness and Birkhead 1984, Birt et al. 1987).

We predicted that due to density-dependent feedback on food supply, cormorants nesting on East Sand Island would on average spend more time foraging and take longer, less frequent foraging trips than reported for Double-crested Cormorants nesting at other colonies (Fowle 1997).

While competition for available forage fish may favor cormorants that forage at a distance from East Sand Island, the diet composition of cormorants that nest on East Sand Island suggests that these adults do not commute up-river to the freshwater zone near Rice Island. Instead, adult cormorants nesting on East Sand Island may commute to foraging areas in the marine zone of the estuary, or perhaps to foraging areas outside the Columbia River estuary altogether (e.g., Willapa Bay or coastal areas).

Due to increasing concern over avian predation on juvenile salmonids in the Columbia River estuary, there is a need to understand how this large and growing cormorant colony exploits the available forage fish resources of the estuary. We sought to investigate which factors affected the foraging patterns exhibited by cormorants nesting at the East Sand Island colony in order to better understand their diet composition and use of forage fish resources.

Sexual differences in foraging patterns are known to occur in several species of seabirds that exhibit sexual dimorphism (reviewed by Weimerskirch et al. 1994), including cormorants from the Southern Hemisphere (Bernstein and Maxon 1984, Wanless et al. 1995, Kato et al.

2000). Diving patterns (Kato et al. 1999, Wanless et al. 1995, Watanuki et al. 1996, Gremillet et al. 1998, Casaux et al. 2001, Ishakawa and Watanuki 2002), trip duration (Cooper 1985), prey type (Gremillet et al. 1998, Ishikawa and Watanuki 2002), and prey size (Kato et al. 1996, Casaux et al. 2001) have all been reported to differ between the sexes in various cormorant species. In the West Coast population *P. a. albociliatus* males are significantly larger than females, including differences in mass (9%; males = 2621 ± 46.8 g, $N = 76$ and females = 2397 ± 25.7 g, $N = 85$; $t_{159} = 4.54$, $P < 0.0001$), culmen length (9%; males = 61.4 ± 0.3 cm, $N = 76$ and females = 57.2 ± 0.2 cm, $N = 85$; $t_{159} = 11.26$, $P < 0.0001$), and culmen depth (9%; males = 15.4 ± 0.08 cm, $N = 76$ and males = 13.5 ± 0.08 cm, $N = 85$; $t_{159} = 16.47$, $P < 0.0001$). This suggests that there may be differences in foraging behaviour between the sexes.

In addition to gender differences, numerous environmental factors may influence the foraging activity of cormorants within an estuarine environment (e.g., Richner 1995, Dorfman and Kingsford 2001). The spatial and temporal foraging patterns of cormorants in this estuary-tidal river system are likely influenced by a variety of natural (e.g., tidal flow, salinity, time of day) and anthropogenic processes (e.g., dam regulated river flow, channel dredging, pile dikes; Collis et al. 2001, Zamon 2000). Tidally-induced foraging patterns have been reported for a variety of estuarine predators, including seabirds (van Tets 1959, Dunn 1975, Richner 1995, Hunt et al. 1998, Irons 1982, Irons 1998, Zamon 2000,

Dorfman and Kingsford 2001). Diurnal foraging patterns have also been reported for many species of Pelecaniformes (e.g., Whitfield and Blaber 1979). Several studies suggest, however, that there is considerable variation, both among sites and among species, in the intensity of cormorant foraging activity throughout the day (see review in Johnsgard 1993).

In this study, we used radio-telemetry to investigate the spatial and temporal patterns in foraging by male and female Double-crested Cormorants nesting on East Sand Island in the Columbia River estuary. We sought to answer the following questions:

1. Do cormorants nesting on East Sand Island forage predominately in marine habitats, as suggested by the proportion of salmonids in the diet compared to cormorants nesting in the freshwater zone of the estuary?
2. Are cormorants nesting on East Sand Island forced to commute long distances to foraging areas to avoid competition with the large numbers of piscivorous waterbirds nesting and roosting on East Sand Island?
3. How is the foraging behaviour of cormorants nesting at East Sand Island influenced by time of day, tidal cycles, seasonal changes, and interannual variability in forage fish availability?

Methods

Study Area

We studied the foraging behaviour of Double-crested Cormorants nesting at the large colony on the western end of East Sand Island. East Sand Island (46°15'45"N, 123°57'45"W) is located in Clatsop County, Oregon, near the mouth of the Columbia River estuary (Figure 2.1). We monitored the foraging distribution of radio-tagged nesting adults over approximately 396 km² of the Columbia River estuary, between the mouth of the Columbia River and Tenasillahe Island (river km 56), and along the southern coast of Washington up to and including Willapa Bay (Figure 2.1). We attempted to include in the survey area all areas potentially used for foraging by cormorants nesting on East Sand Island, based on published records of the maximum foraging range for nesting Double-crested Cormorants (40 km; Custer and Bunck 1992) and previous observations of foraging cormorants in the Columbia River estuary and along the adjacent coastline (Roby et al. 1998, Collis et al. 1999).

For analysis purposes, we subdivided the estuary into 3 major zones corresponding to areas of marine (ca. river km 0 to 12), estuarine-mixing (ca. river km 12 to 29), and freshwater (above ca. river km 29) salinities (*sensu* Simenstad et al. 1990; Figure 2.2). These salinity zones are not static; salinity levels vary with a number of environmental parameters, including river flow, tide stage, and tide series (i.e., spring vs. neap; Jay and Smith 1990, Simenstad et al. 1990). The salinity zones

represent, however, large-scale habitats known to strongly influence the distribution of fish assemblages in the Columbia River estuary (Haertel and Osterberg 1967, Bottom et al. 1984, Bottom and Jones 1990), and likely influence cormorant foraging distribution as well. The cormorant colony on East Sand Island is located within the marine zone, at least 5 km from the estuarine-mixing zone, and at least 20 km from the freshwater zone (Figure 2.2).

Radio tagging

We studied the foraging patterns of radio-tagged Double-crested Cormorants nesting on East Sand Island between 1 June and 26 July in 2000 and 2001. Early in the 2000 and 2001 nesting seasons, we captured and radio-tagged a total of 85 adult Double-crested Cormorants at the East Sand Island colony. We trapped adults on dark (i.e., moonless or cloudy), cool, and dry nights from mid to late May, when cormorants were attending nests during egg-laying and early incubation. Adult cormorants were spotlighted on the colony using water-resistant, hand-held spotlights (12-V; 1 M candlepower) and captured using aluminum, hand-held fish landing nets (1.5-m extendable pole with 0.75-m hoop). Captured individuals were immediately placed in cotton bags and transported to holding crates located at an off-colony location, where they were held until processing.

Fig 2.1

Fig 2.2

Radio-transmitters (150-152 MHz, 45 pulses per minute, Advanced Telemetry Systems [ATS], Insanti, Minnesota, USA) weighing 10 g (0.4% of average adult cormorant body mass) were attached to 35 cormorants in 2000 and 50 cormorants in 2001. Transmitters had an estimated battery life of 80 d and were equipped with a mortality switch. Transmitters were affixed ventrally at the base of the four central retrices using two cable ties and Loctite® superglue (*sensu* Anderson and Ricklefs 1987). Radio-tagged cormorants were then marked with patagial tags made of brightly coloured vinyl-coated fabric (fluorescent orange in 2000 and bright pink in 2001) and numbered with a unique 2-digit number (as per J. Coleman, Cornell University, pers. comm.) to aid in behavioural observations from blinds located on the periphery of the cormorant colony in order to verify nesting status.

In 2000, radio-tagged cormorants were sexed using a discriminant function model incorporating culmen length, culmen depth, and flattened wing length of known-sex birds (cf. Glahn and McCoy 1995, Jodice et al. 2000); the model predicted sex with >95% accuracy (C. Anderson, unpubl. data). In 2001, radio-tagged cormorants were sexed using blood samples ($\leq 250 \mu\text{l}$) collected from the tarsal vein. Blood was stored in cryogenic tubes containing a buffer solution (100 mM Tris HCl pH 8.0, 100 mM EDTA pH 8.0, 10 mM NaCl, 0.5% SDS) until shipment to Celera AgGen (Davis, CA) for molecular sexing.

Spatial foraging patterns

Between 1 June and 26 July, we conducted 20 and 17 biweekly aerial telemetry surveys in 2000 and 2001, respectively (survey area depicted in Figure 2.1). During each survey, we attempted to relocate each actively-nesting, radio-tagged cormorant using a fixed-wing aircraft (Cessna 206) equipped with an antenna mounted on each wing and a switch box system to isolate signal location. To reduce potential sampling biases (White and Garrott 1990), we randomly selected the starting point for each telemetry survey. From our starting point, we flew in the most direct flight path to cover the water-bodies (river channels, bays, coastline) of the entire survey area during each flight; we did not survey areas more than once per flight (i.e., if we flew over the same region of the river twice for logistical purposes we did not search for radio-tagged birds the second time). We used a VHF receiver (R4000, ATS) to continuously scan for each radio-tagged cormorant (ca. 5 sec per frequency). Once a radio frequency was detected, we tracked the individual until we were close enough to fix a position. A bird was considered relocated when the strength of its transmitter signal was continuous while circling and using only one antenna. A Global Positioning System (GPS) receiver was used to determine coordinates (latitude and longitude) of the relocation.

The error ellipse associated with locating a radio-tagged cormorant averaged $0.50 \text{ km} \pm 0.13 \text{ km}$, based on 3 trials of locating transmitters ($N = 7$) at fixed positions in the estuary that were unknown to the radio-

trackers. Relocations were not sufficiently precise to assign a foraging habitat to each relocation, but were used to determine the salinity zone used by foraging cormorants and their distance from the colony. Radio-tagged cormorants were removed from the sample when (1) their nest failed, (2) the radio-tag transmitted a mortality signal, (3) the wing-tagged cormorant was observed on-colony without its radio-tag, or (4) the signal was repeatedly relocated at the same site (repeated relocations were eliminated from the data set retroactively).

Temporal foraging patterns

In 2001, we continuously monitored the colony attendance patterns of actively-nesting radio-tagged cormorants between 1 June and 26 July. Temporal attendance patterns (i.e., frequency and duration of colony absences, proportion of time spent off-colony) were assessed using two fixed receiving stations located at the edge of the colony (*sensu* Suryan et al. 2002). Fixed receiving stations consisted of a VHF receiver (R4000, ATS) connected to a data collection computer (DCC II, ATS). Each receiving station was powered by a 12-V deep-cycle marine battery connected to a solar panel. A 2-element “H” antenna was connected to each receiver and oriented to provide approximately 1.0 km horizontal reception range and approximately 1.5 m vertical reception range (equivalent to the maximum range in elevation of nests). The receiver scanned for each transmitter frequency for 20 sec; cycle duration to scan

all programmed frequencies ranged between 13.3 and 18.5 min. Once a signal was detected, the DCC logged the radio-transmitter frequency and the time. The receivers were also programmed to scan for two reference transmitters (i.e., radio-tags placed on the colony) and three non-existent transmitter frequencies each cycle to validate detections by the receivers. For our analyses, we included only those cycles where both reference frequencies were detected and none of the non-existent frequencies were detected (92% of cycles qualified for analyses). Only those radio-tagged cormorants that were observed nesting for a minimum period of 7 days (mean = 40.1 ± 3.0 d, $N = 33$, range = 9 to 56 d) were included in subsequent analyses.

Data Analysis

Spatial foraging patterns

We estimated the proportional use of the three salinity zones within the Columbia River estuary by radio-tagged cormorants actively-nesting on East Sand Island during June and July of 2000 and 2001. To account for the potential lack of independence between observations made on the same individual (e.g., Kenward 1992), we randomly sub-sampled our data set so that each individual contributed one aerial telemetry relocation to the following analyses ($N = 45$). We tested for an association between time (year*month) and the distribution of aerial telemetry relocations among the three salinity zones of the Columbia River estuary for both

male ($N = 29$) and female ($N = 16$) radio-tagged cormorants using Fisher's exact tests (SAS 1999). Subsequently, inter-annual, monthly, and gender differences in distribution of radio-tagged cormorants among the three salinity zones were examined using chi-square tests (SAS 1999).

To determine if relocations for individuals that were relocated ≥ 5 times were randomly distributed throughout the estuary, we used a chi-square test of the observed mean nearest neighbour distance and the expected

$$[0.5*\sqrt{(A/N_i)}],$$

where A = the area of the estuary and N_i = the number of relocations for individual i (*sensu* Boots and Getis 1978). To determine if relocations for particular individuals had a clumped rather than regular spatial distribution throughout the estuary, we compared expected values to observed values of mean nearest neighbour distance. Additionally, we used a Wilcoxon rank-sum test to determine if there was a difference in median foraging range (straight-line distance between the relocation and the East Sand Island colony) between the sexes.

Temporal foraging patterns

We attempted to distinguish between short absences from the colony when breeding adults collected nest material or bathed (mean duration = 16.0 ± 1.62 min, $N = 36$, range = 1 to 31 min) and longer absences that represented foraging trips, based on behavioural

observations made during the 2001 nesting season. Because cormorants are believed to be exclusively diurnal foragers (Mendall 1936, Schreiber and Clapp 1987), we only considered colony absences between 04:00 and 22:00 PDT as potential foraging trips. During 1 June to 26 July of 2001, sunrise occurred between 05:23 and 05:50 PDT and sunset occurred between 20:52 and 21:11 PDT; civil twilight occurred between 04:44 and 05:15 PDT and between 21:28 and 21:49 PDT (USNO 2002). Therefore, foraging trips were defined as colony absences lasting at least 2 scanning cycles (>13.3 min) that occurred between 04:00 and 22:00 PDT, and did not exceed 1 d. Using these criteria, absences from the colony lasting as long as 37 min could potentially be classified as non-foraging trips.

We examined temporal foraging patterns on two scales: long-term (seasonal) and short-term (diurnal and tidal). First, we considered seasonal effects on temporal foraging patterns, while controlling for gender effects. We calculated means for both months of the study period (June and July) for all response variables for each radio-tagged cormorant; 19 radio-tagged birds (8 females and 11 males) were included in the analysis ($N = 19 \text{ birds} \times 2 \text{ months} = 38 \text{ observations}$). Because there were only 2 repeated measures, the Huynh-Feldt conditions were automatically satisfied, so that the analysis could proceed as a split-plot-in-time model with gender as the between-bird factor, and time and time*gender as the within-bird factors (Keuhl 2000). We used two-way

ANOVAs to investigate the effects of gender, month, and their interaction on the three response variables: average trip duration, total daily foraging time, and frequency of foraging trips.

Second, we considered the short-term effects of time of day and tidal cycles by exploring how the proportion of time spent foraging changed with time of day, tide stage, and tide series during the month of June, while controlling for gender. Data on proportion of time spent foraging were expressed as the proportion of detection cycles when the transmitter signal was not detected by the on-colony receiving station (see Methods) for each combination of time of day, tide stage, and tide series. We excluded short absences (1 scanning cycle) from the dataset prior to analyses and we only considered data collected in June to avoid potential bias due to increased tag loss in July. We separated time of day into three 6-hr time periods: morning (04:00 -10:00), mid-day (10:00 -16:00), and evening (16:00 - 22:00). We considered two categories of tide stage (ebb or flood), and two categories of tide series (neap or spring).

For each of 32 radio-tagged cormorants (14 females and 18 males) that were actively-nesting throughout June, we calculated the mean proportion of time spent foraging so that each cormorant contributed to each of the time of day and tidal cycle categories described above ($N = 12$ categories in total); the categories for each cormorant constitute a multivariate response with a three-way factorial structure ($3 \times 2 \times 2$). Gender is a between-bird factor while the 3 main effects (time of day, tide stage,

and tide series) and 4 interaction effects in the three-way structure are within-bird factors. Each of the 7 factorial effects from the three-way structure (along with its interaction with gender) had its own error term (which is equivalent to analyzing each within-bird factorial effect separately). For the within-bird factorial effects having a single d.f. (e.g., main effect of tide series and interaction between tide series and gender), the analysis reduces to a split-plot type model with an error term representing the variation in the factorial effect across the birds within each gender (30 d.f., with $14-1=13$ from females and $18-1=17$ from males). For within-bird factorial effects having 2 d.f. (e.g., main effect of time of day and interaction between gender and time of day), both a more liberal split-plot type test was used (with $2*30 = 60$ d.f. for the within-bird error term) as well as a more conservative MANOVA test (does not require the Huynh-Feldt assumptions; Kuehl 2000). Because in each case both tests supported the same conclusions, only the simpler split-plot type tests were reported. Because of unequal numbers of males and females, Type III sums of squares were used for testing main effects and interactions (SAS 1999).

We accounted for potential differences among individuals of the same sex (Gremillet et al. 1998, Ballard et al. 2002) by using a nested classification of individual cormorant within the levels of sex (Ramsey and Schafer 1997). All response variables yielded normal distributions and

homogeneous variance. For all tests of significance we used an alpha-level of 0.05 and reported two-tailed *P*-values.

Results

Of the 85 radio-tagged individuals, 58 (68%) were males and 27 (32%) were females. This bias in sex ratio of radio-tagged individuals likely reflects more pronounced territorial behaviour by nesting male cormorants early in the nesting season (Hatch and Weseloh 1999). Of the radio-tagged individuals, 56 (66%) were subsequently verified to be nesting through direct observation from blinds and were radio-tracked throughout the respective study periods; 34 (61%) were males ($N = 16$ in 2000, $N = 18$ in 2001) and 22 (39%) were females ($N = 7$ in 2000, $N = 15$ in 2001).

Spatial foraging patterns

We relocated foraging radio-tagged cormorants that were nesting on East Sand Island 138 and 48 times during the 2000 and 2001 nesting seasons, respectively (Figure 2.3). Males were relocated off-colony twice as often as females ($N = 125$ relocations and $N = 61$ relocations, respectively). The sex bias in number of relocations is primarily because there were more than twice as many males as females radio-tracked in 2000, when the majority of relocations were made.

Fig 2.3

Forty-five (80%) of radio-tagged nesters ($N = 56$) were relocated at least once while off-colony (and presumably foraging) during the season when they were radio-tagged; of those radio-tagged nesters, the average number of relocations was 4.04 (SE = 0.47, $N = 45$, range = 1 - 12). No radio-tagged cormorants that were known to be nesting were relocated outside of the Columbia River estuary (i.e., in Willapa Bay or along the coast) in either 2001 or 2002 (Figure 2.1). All off-colony relocations occurred >0.50 km from the nesting colony and, therefore, outside the average error ellipse associated with transmitters on the cormorant colony.

After accounting for potential autocorrelation between foraging relocations for each individual, we found no association between month, year, or their interaction (year*month) and the distribution of the sub-sample of aerial telemetry relocations ($N = 45$) among the three salinity zones of the Columbia River estuary either for males ($N = 29$, Fisher's exact test: $P = 0.66$) or for females ($N = 16$, Fisher's exact test: $P = 0.89$). The distribution in the sub-sample of foraging locations of the within the three salinity zones was similar between the 2000 and 2001 breeding seasons ($\chi^2_2 = 1.68$, $P = 0.43$); therefore, we combined the data from the two years for further analyses. For all the relocations ($N = 186$), the distribution among the salinity zones was as follows: 51 (27%) in the marine zone, 66 (35%) in the estuarine zone, and 69 (37%) in the freshwater zone (Figure 2.3). There was no difference between months

(June vs. July) in the distribution of sub-sampled relocations among zones ($\chi^2_2 = 0.751$, $P = 0.69$). There was a considerable difference, however, between the sexes in the spatial distribution of the sub-sample of relocations among the three salinity zones in the Columbia River estuary ($\chi^2_2 = 18.49$, $P < 0.0001$). Overall, most of the relocations of radio-tagged females were within the estuarine-mixing zone (66%, $N = 40$, 0.34 relocations/km²), followed by the marine zone (28%, $N = 17$, 0.19 relocations/km²), and freshwater zone (7%, $N = 4$, 0.02 relocations/km²). In contrast, most relocations of radio-tagged males were within the freshwater zone (52%, $N = 65$, 0.35 relocations/km²), followed by the marine zone (27%, $N = 34$, 0.29 relocations/km²), and the estuarine-mixing zone (21%, $N = 26$, 0.29 relocations/km²).

Nesting males commuted significantly greater distances (mean = 15.98 ± 0.72 km) from East Sand Island to forage than nesting females (mean = 8.93 ± 0.55 km; $Z_{228} = 5.94$, $P < 0.0001$). The majority of off-colony relocations for females were <10 km from the nesting colony, whereas the majority of off-colony relocations for males were >15 km from the nesting colony (Figure 2.4). Two off-colony relocations of actively-nesting males were at distances >40 km from the colony (41.9 km and 47.2 km). To our knowledge, these distances exceed previously published records of the maximum foraging range for nesting Double-crested Cormorants (c.f. 40 km; Custer and Bunck 1992).

There was strong evidence that the relocations for individual radio-tagged cormorants were not randomly distributed throughout the study area ($\chi^2_{15} = 6747.67, P < 0.0001$). Fourteen out of the 16 individuals that were relocated ≥ 5 times off colony (88%) had observed values that were less than expected values of mean nearest neighbour distance, indicating that individual relocations had a clumped rather than regular spatial distribution throughout the estuary. Figure 2.5 depicts the off-colony detections for two radio-tagged nesting adults, a female and a male, that were repeatedly detected in the same foraging areas.

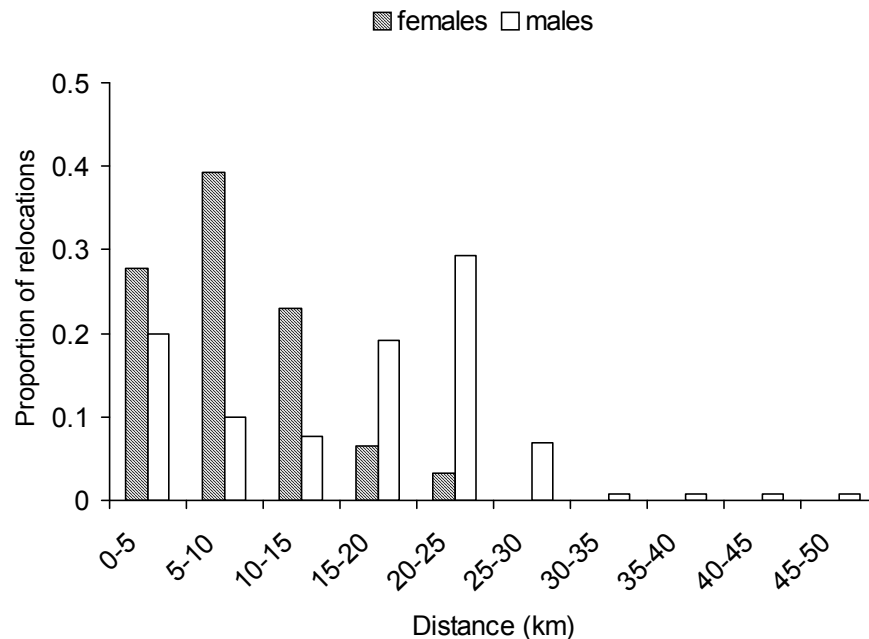


Figure 2.4. Proportion of total off-colony relocations for female ($N = 61$) and male ($N = 125$) radio-tagged Double-crested Cormorants in each 5-km interval (straight-line distance) from the nesting colony on East Sand Island in the Columbia River estuary. All relocations were from aerial telemetry surveys conducted during the 2000 and 2001 nesting seasons.

Fig 2.5

Temporal foraging patterns

Average foraging trip duration was significantly greater for females than for males ($F_{1,17} = 6.73$, $P = 0.02$; Table 2.1), although there was no difference between the sexes in total time spent foraging after controlling for differences due to month ($F_{1,17} = 0.82$, $P = 0.38$; Table 2.1).

Furthermore, males went on more foraging trips compared to females ($F_{1,17} = 10.06$, $P = 0.006$; Table 2.1). This suggests that females compensated for fewer foraging trips by taking longer trips compared to males.

There was no statistical difference in average trip duration ($F_{1,17} = 0.03$, $P = 0.86$) or total time spent foraging ($F_{1,17} = 3.22$, $P = 0.09$) between June and July, after controlling for gender differences; however, there was a tendency for cormorants to spend more total time foraging in June than in July (Table 2.1). There was no evidence of an interaction effect of sex*month on average trip duration or total time spent foraging ($F_{1,17} = 1.01$, $P = 0.33$ and $F_{1,17} = 2.65$, $P = 0.12$, respectively). There was convincing evidence, however, of an interaction effect of sex*month on frequency of foraging trips ($F_{1,17} = 6.66$, $P = 0.02$); females went on more foraging trips in June than in July, whereas males went on more foraging trips in July compared to June.

There was a significant short-term effect on proportion of time spent foraging due to time of day ($F_{2,60} = 27.19$, $P < 0.0001$) and tide stage ($F_{1,30} = 34.77$, $P < 0.0001$), regardless of sex (Table 2.2). There was also a

significant 3-way interaction effect of daytime*tide stage*tide series on proportion of time spent foraging ($F_{2,60} = 59.69$, $P < 0.0001$; Table 2.2). Nesting cormorants spent a greater proportion of time foraging during morning ebb tides in spring tide series, but during evening ebb tides in neap tide series (Figure 2.6).

Discussion

Spatial patterns

Radio-tagged Double-crested Cormorants nesting on East Sand Island usually commuted at least 5 km to forage in the shallow bays, tidal flats, and nearshore areas of the estuarine-mixing zone and freshwater zone, rather than the marine zone that surrounds the nesting colony (Figure 2.3). Of the three salinity zones, the estuarine-mixing zone is reported to have the greatest average densities of fishes (Bottom and Jones 1990), especially in shallow bays and nearshore environments (Jones et al. 1990, Bottom and Jones 1990). The observed distribution of foraging cormorants is also consistent with localized depletion of forage fishes by the large numbers of piscivorous waterbirds nesting and roosting on East Sand Island.

Table 2.1. Average foraging trip duration (hrs; A), time spent foraging (hrs/d; B) and frequency of trips (trips/d; C) for male and female Double-crested Cormorants nesting on East Sand Island during June and July of 2001. Results of two-way repeated measures ANOVAs are expressed as means \pm SE. NB: day unit refers to the 18-hr daytime period (04:00 – 22:00) considered for these analyses.

A.			
	Females (<i>N</i> = 8)	Males (<i>N</i> = 11)	
June	2.56 \pm 0.28	1.94 \pm 0.24	2.25 \pm 0.18
July	2.72 \pm 0.28	1.71 \pm 0.24	2.21 \pm 0.18
	2.64 \pm 0.24	* 1.82 \pm 0.20	ns
B.			
June	3.39 \pm 0.42	3.01 \pm 0.36	3.20 \pm 0.28
July	1.93 \pm 0.42	2.94 \pm 0.36	2.43 \pm 0.28
	2.66 \pm 0.26	ns 2.97 \pm 0.22	ns
C.			
June	1.46 \pm 0.20	1.61 \pm 0.17	1.53 \pm 0.13
July	0.65 \pm 0.20	1.74 \pm 0.17	1.20 \pm 0.13
	1.06 \pm 0.15	** 1.67 \pm 0.13	ns

ns = not significant; * 0.05 > *P* > 0.01; ** *P* < 0.01

Table 2.2

Fig 2.6

Gender differences in foraging distribution were particularly pronounced. Although most of the off-colony relocations of radio-tagged females were in the estuarine-mixing zone, most off-colony relocations of males were in the freshwater zone. This finding was unexpected because the freshwater zone of the Columbia River estuary is the furthest from the nesting colony on East Sand Island and is reported to have lower densities of fish than the other two zones (Bottom and Jones 1990). Many of the predominant species in the assemblage of schooling forage fishes in the estuary are restricted to the marine and estuarine-mixing zones, such as Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), Pacific tomcod (*Microgadus proximus*), and Pacific sardine (*Sardinops sagax*) (Bottom and Jones 1990). Nesting male cormorants presumably commuted significantly greater distances to forage in areas of the estuary that are generally less productive in order to exploit predictable prey resources or foraging opportunities not available in the other two zones.

Male cormorants are reported to utilize a wider array of foraging techniques than females, which may allow them to exploit a wider variety of prey (Gremillet et al. 1998). Males may commute greater distances to use foraging sites where they are able to forage individually on larger demersal prey (Voslamber 1995, Ishikawa and Watanuki 2002). Solitary foraging has been reported as an efficient foraging strategy for cormorants to pursue evasive prey (e.g., demersal fishes that conceal themselves in

bottom sediments; Voslamber et al. 1995). Double-crested Cormorants are believed to probe bottom sediments to locate and capture hidden prey (Voslamber et al. 1995, Hatch and Weseloh 1999) and have been reported to shift to solitary foraging behaviour when the water is turbid (Custer and Bunck 1992, Van Eerden and Voslamber 1995).

Findings from a concurrent study of diet composition (% of identifiable fish biomass in stomach contents) in Double-crested Cormorants nesting on East Sand Island support the hypothesis that males employ a wider array of foraging tactics than females and have a greater tendency to pursue benthic prey. During 2000 and 2001, the diet of males consisted of a significantly greater proportion of demersal prey (i.e., flounder) compared to the diet of females ($\chi^2_1 = 5.42$, $P = 0.02$; D. Roby, unpubl. data). Starry flounder (*Platichthys stellatus*) were more than twice as prevalent in the diet of males (25%) than in that of females (Figure 2.7), although the difference was not statistically significant (exact Wilcoxon rank-sum test: $P = 0.19$). Starry flounder are reported to travel up into the tidal-fluvial regions of rivers (Morrow 1980), perhaps due to higher standing stocks of benthic infauna than in the estuarine-mixing zone (Jones et al. 1990). This species avoids predators by hiding in the sand on the bottom and assuming cryptic colouration (Orcutt 1950).

Pacific sand lance (*Ammodytes hexapterus*) were significantly more prevalent in the diet of males than in that of females (exact Wilcoxon rank-sum test: $P = 0.03$; Figure 2.7). Pacific sand lance are also known to bury

themselves in sediment during the day to avoid predators (Emmett et al. 1991). Our findings are consistent with a recent study of Japanese Cormorants (*P. capillatus*), which found that males foraged more on demersal fishes than did females (Ishikawa and Watanuki 2002). A high proportion of both male and female diets, however, consisted of schooling marine forage fishes (D. Roby, unpubl. data). Pacific herring, Pacific sardine, and northern anchovy combined comprised 30% and 40% of male and female diets, respectively (Figure 2.7). These schooling forage fishes are predominately found in the estuarine-mixing zone of the estuary (Bottom and Jones 1990) and were likely secured through social foraging techniques (Van Eerden and Voslamber 1995, Gremillet et al. 1998). Hence, males may participate in communal foraging strategies to garner schooling prey (Gremillet et al. 1998, Ishikawa and Watanuki 2002). Males may join foraging flocks of conspecifics or mixed-species assemblages (Van Eerden and Voslamber 1995, Hatch and Weseloh 1999, Zamon 2000) encountered while commuting to traditional foraging areas in the upper estuary.

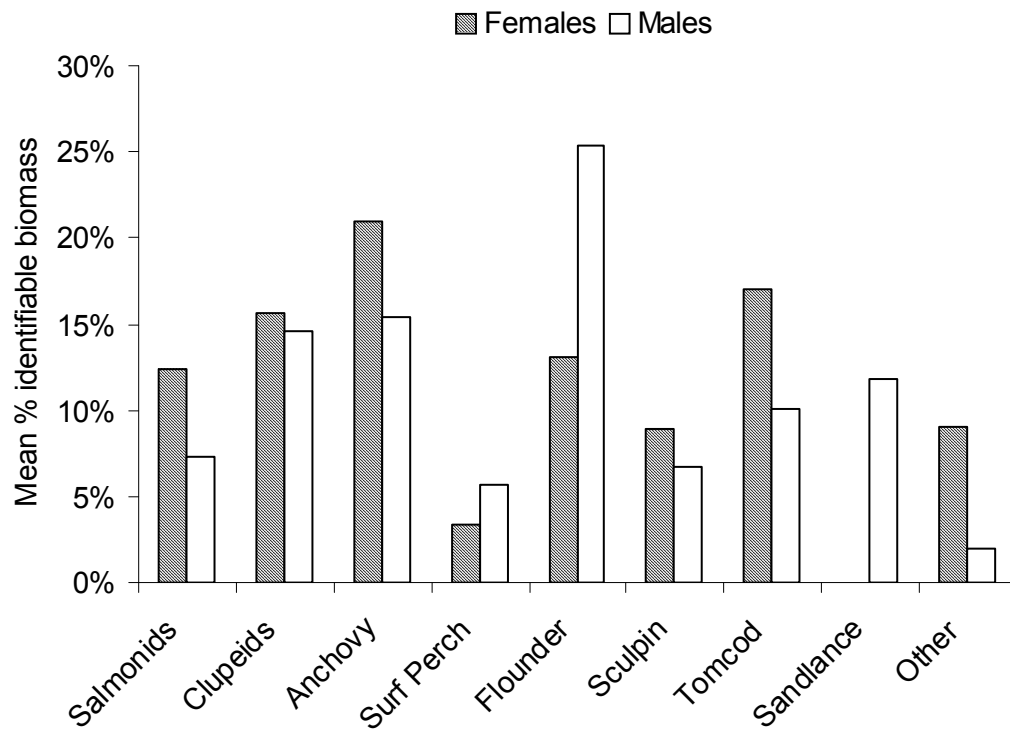


Figure 2.7. Diet composition (mean % identifiable fish biomass) of collected female ($N = 25$) and male ($N = 40$) Double-crested Cormorants nesting at East Sand Island in June of 2000 and 2001 (D. Roby, unpubl.data).

Females took longer foraging trips than did males, suggesting the more restricted foraging range of females was not a reflection of time constraints. Females may have been energetically constrained, however, due to the higher investment by females in egg production and incubation (Carey 1996), which may have precluded longer distance foraging trips. Also, the smaller size of females implies a higher cost of transport than in males. Consistent with results from this study, activity budgets of South

Georgian Shags (*Phalacrocorax georgianus*) revealed that males spent more time flying than females (Wanless et al. 1995). Flight is an energetically-expensive activity in species with high wing-loading, such as cormorants (Pennycuick 1975).

Optimal foraging theory predicts that because male cormorants flew significantly farther to forage and took more foraging trips than females, males should somehow compensate for this additional energy expenditure (Krebs 1978). Avoiding competition for food with females or gaining access to more easily captured or higher energy prey (Maurer 1996) are potential explanations for the observed patterns of male foraging. Furthermore, these sexual differences in foraging behavior may be influenced by other factors not investigated in this study. Male and female cormorants may have different foraging capabilities related to the sexual dimorphism in this subspecies. Differences in diving capacity, bill size, and pharyngeal opening may allow the sexes to efficiently exploit different habitats and/or prey types (Selander 1966, Maurer 1996).

Temporal patterns

Double-crested Cormorants nesting at East Sand Island also exhibited sexual differences in foraging patterns that changed as the nesting season progressed. The higher foraging intensity of males in July suggests that males may bear a greater proportion of chick provisioning duties late in chick-rearing compared to females. Gender differences in

foraging intensity may also help ensure that the nest site is defended more by the larger male at times when nest contents are most vulnerable to predators, such as during the incubation or brooding periods (Hatch and Weseloh 1999).

Our findings suggest that foraging is more productive for nesting Double-crested Cormorants during ebb tides. Similarly, Dunn (1975) reported that Double-crested Cormorants in New Hampshire fed their young more during ebb tides and van Tets (1959) reported that Double-crested Cormorants foraged in channels during ebb tides in British Columbia. There are likely two reasons for this foraging pattern. First, receding water during ebb tides can concentrate benthic fishes, such as flounder, in shallow bays, shoals, and nearshore environments and make them more conspicuous (Wirjoatmodjo and Pitcher 1984, Raffaelli et al. 1990). Richner (1995) reported that Great Cormorants (*P. carbo*) foraged most actively during ebb tides when foraging was predominately on flounder. Flounder have been shown to follow ebb tides as they forage, perhaps to avoid increased risks of stranding and depredation by piscivorous birds (Wolff et al. 1981, Reise 1985, Wirjoatmodjo and Pitcher 1984).

Second, in the Columbia River estuary, tidal currents are markedly stronger during ebb tide due to the combination of tidal flow and river discharge (CO-OPS 2002), and plankton distribution in estuaries is known to be strongly associated with tidal currents (Trinast 1975). Because a

large proportion of cormorant prey is comprised of planktivorous fishes (e.g., clupeids, anchovies; Collis et al. 2002), it is likely that cormorants are foraging during ebb tide to follow the tide-influenced movements of their planktivorous prey. Alldredge and Hamner (1980) reported that plankton biomass and density were greatest in nearshore and shallow areas located in the lee of points of land that created eddies. Off-colony relocations of cormorants in the estuary were often either in close proximity to the shoreline and/or in association with structures that create eddies, such points of land (Figure 2.3), pile dikes, and jetties (Collis et al. 2001).

To our knowledge no other studies of cormorant foraging patterns have found an effect of tide series (Richner 1995, Dorfman and Kingsford 2001), although tide series is known to influence the foraging patterns of other piscivorous seabirds (Irons 1982, Irons 1998). The reason for the relationship between foraging patterns and tide series is not clear. Foraging patterns may be influenced by the extent of saltwater intrusion within the estuary, which is known to influence the distribution of marine forage fishes (Bottom and Jones 1990). Salinity intrusion is greater during neap tide series compared to spring tide series in the Columbia River estuary, despite smaller tidal incursion on neap tides (Jay and Smith 1990). The reduced vertical mixing during neap tides reduces friction between salt and freshwater layers and permits greater saltwater intrusion (Jay and Smith 1990); hence, greater incursion into the upper estuary by

marine forage fishes may occur during neap tides. Furthermore, the increased turbidity associated with spring tides (Jay and Smith 1990) may alter the distribution of forage fishes in the estuary and the behaviour of foraging cormorants.

Prey availability and diet

Marine forage fishes were notably more abundant in the Columbia River estuary in 2001 as compared to previous years (Brodeur et al. in review, R. Emmett, NMFS, unpubl. data). Data on cormorant diets in 2001 indicated that the large breeding colony on East Sand Island relied mostly on schooling marine forage fishes for food. The high availability of marine forage fishes suggests that nesting adult cormorants should have taken fewer foraging trips of shorter duration and spent less total time foraging and more time attending the nest. Our findings support these hypotheses; cormorants nesting at East Sand Island spent on average only 16% of daylight hours foraging during the 2001 nesting season. This is a much lower proportion of time spent foraging than reported for Double-crested Cormorants nesting on Lake Champlain, Vermont (44%; Fowle 1997). Our findings suggest that prey-depletion and/or competition for food resources was not a major factor during this year of high marine forage fish availability. Despite the apparent abundance of forage fish within short distances of the East Sand Island colony, breeding adults

(especially males) commuted substantial distances to forage in the estuarine-mixing and freshwater zones.

A recent study of the diet composition of Double-crested Cormorants nesting in the Columbia River estuary showed that the diet of cormorants nesting on Rice Island, located in the freshwater zone, included a substantially higher proportion of salmonids compared to the diet of cormorants nesting on East Sand Island, located in the marine zone (three times more by mass; Collis et al. 2002). These findings suggest that cormorants foraging in the freshwater zone consume more salmonids than cormorants foraging in the marine or estuarine-mixing zones. Furthermore, there was a pronounced seasonal decline in the proportion of salmonids in the diet of cormorants nesting at Rice Island; most salmonids were consumed during the peak out-migration of salmonid smolts that occurred early in the nesting season (April and May) and much less late in the nesting season (June and July; Collis et al. 2002).

Results from our study revealed that, during June, male cormorants foraged predominately in the freshwater zone near Rice Island. This suggests that males should consume more juvenile salmonids compared to females. Contrary to expectation, however, males tended to have a lower proportion of salmonids in their diet during June compared to females (Figure 2.7); however, the difference was not significant (exact Wilcoxon rank-sum test: $P = 0.86$; SAS 1999). An important caveat is that the data presented here on diet composition of cormorants nesting on

East Sand Island were from only June of 2000 and 2001, and thus after the peak out-migration by salmonid smolts (FPC 2002). We used only the June diet data to gain a better understanding of how prey types may be related to cormorant foraging patterns during the radio-tracking study. The proportion of salmonids in cormorant diets was greater in May (22%, $N = 71$) than in June (6%, $N = 84$) of 2000 and 2001, but the difference was only marginally significant (exact Wilcoxon rank-sum test: $P = 0.09$). Nevertheless, these results support the conclusion that salmonids represent a greater proportion of cormorant diets during peak out-migration of salmonid smolts. During April and May East Sand Island cormorants, especially males, may forage even more in the freshwater zone and rely more on salmonid smolts as a food source than they do in June and July.

Seabird diets are known to vary in response to changing oceanic conditions (Montevecchi and Myers 1996, Montevecchi and Cairns 2002). We predict that in years when stocks of marine forage fish within the estuary become depressed (due to El Niño perturbations or poor ocean conditions; Bayer 1986, Emmett and Brodeur 2000), Double-crested Cormorants may become more reliant on the more predictable fish resources of the estuary, such as the 150-200 M hatchery-reared salmonid smolts that are released annually (FPC 2002). Because male cormorants were frequently relocated foraging in the upper estuary, despite the high availability of marine forage fishes in the estuarine-mixing

zone, males may forage in the freshwater zone of the estuary more during years of low availability of marine forage fish. The freshwater zone is recognized as an important transition area for juvenile salmonids during smoltification (Emmett et al. 1991). Juvenile salmonids may be more vulnerable to cormorants, particularly male cormorants, during El Niño perturbations or poor ocean conditions. Furthermore, because breeding cormorants spent only a small proportion of their available time foraging in 2001, it appears that they can increase foraging effort and reduce colony attendance in response to lower availability of marine forage fish.

The ability to commute considerable distances to forage in areas of high prey availability, gender differences in foraging distribution, and the ability to forage on a wide variety of schooling prey are all important attributes for a colonial nesting species that forages on highly variable food resources (Ashmole 1967, Birt et al. 1987). The foraging patterns of Double-crested Cormorants demonstrated in this study may be critical for this large and growing colony to remain productive when forage fish stocks become more limited and competition with many thousands of other nesting and roosting piscivorous waterbirds becomes more stringent.

Literature Cited

- Allredge, A.L., and W.M. Hamner. 1980. Recurring aggregation of zooplankton by a tidal current. *Estuarine and Coastal Marine Science* 10:31-37.
- Anderson, D.J., and R.E. Ricklefs. 1987. Radio-tracking Masked and Blue-footed boobies (*Sula* spp.) in the Galapagos Islands. *National Geographic Research* 3:152-163.
- Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-473.
- Ballard, G., D.G. Ainley, C.A. Ribic, and K.R. Barton. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adelie Penguins. *Condor* 103:481-490.
- Bayer, R.D. 1986. Seabirds near an Oregon estuarine salmon hatchery in 1982 and during the 1983 El Niño. *Fishery Bulletin* 84:279-286.
- Bernstein, N.P., and S.J. Maxson. 1984. Sexually distinct daily activity patterns of Blue-eyed Shags in Antarctica. *Condor* 86:151-156.
- Birt, V.L., T.P. Birt, D.K. Cairns, and W.A. Montevecchi. 1987. Ashmole's halo: Direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40:205-208.
- Blackwell, B.F., W.B. Krohn, N.R. Dube, and A.J. Godin. 1997. Spring prey use by Double-crested Cormorants on the Penobscot River, Maine, USA. *Colonial Waterbirds* 20:77-86.
- Boots, B., and A. Getis. 1978. Point pattern analysis. Sage Publications, London, UK. 93 pp.
- Bottom, D.L., K.K. Jones, and M.J. Herring. 1984. Fishes of the Columbia River estuary. Final report on the Fish Work unit of the Columbia River Estuary Data Development Program. Oregon Department of Fish and Wildlife, Corvallis, OR. 113 pp.
- Bottom, D.L., and K.K. Jones. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. *Progress in Oceanography* 25:243-270.

- Brodeur, R., W.G. Pearcy, and S. Ralston. *In review*. Abundance and distribution patterns of nekton and micronekton in the Northern California current transition zone. *Journal of Oceanography*.
- Carey, C. 1996. Female reproductive energetics. Pages 324-374 *in* Carey, C. (ed.), *Avian energetics and nutritional ecology*. Chapman & Hall, New York, NY. 543 pp.
- Carter, H.R., A.L. SOWLS, M.S. Rodway, U.W. Wilson, R.W. Lowe, G.J. McChesney, F. Gress, and D.W. Anderson. 1995. Population size, trends, and conservation problems of the Double-crested Cormorant on the Pacific Coast of North America. *Colonial Waterbirds* 18 (Special Publication 1):189-215.
- Casaux, R., M. Favero, P. Silva, and A. Baroni. 2001. Sex differences in the diving depths and diet of Antarctic Shags at the South Shetland Islands. *Journal of Field Ornithology* 72:22-29.
- Collis, K., S.L. Adamany, D.D. Roby, D.P. Craig, and D.E. Lyons. 1999. Avian predation on juvenile salmonids in the lower Columbia River. 1998 Annual Report of the Oregon Cooperative Fish and Wildlife Unit at Oregon State University to Bonneville Power Administration and U.S. Army Corps of Engineers, Portland, OR. 148 pp.
- Collis, K., M. Hawbecker, D.D. Roby, C. Couch, J. Wolf, and C.D. Anderson. 2001. Pelican, cormorant, and pinniped use of pile dikes and jetties at the mouth of the Columbia River estuary, 2000. Unpublished report, Oregon State University, Corvallis, OR. 39 pp.
- Collis, K., D.D. Roby, D.P. Craig, S.L. Adamany, J.Y. Adkins, and D.E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537-550.
- CO-OPS (Center for Operational Oceanographic Products and Services). 2002. Hourly water level predictions for Astoria, OR, 2000 and 2001. NOAA, NOS. At <http://co-ops.nos.noaa.gov>.
- Custer, T.W., and C. Bunck. 1992. Feeding flights of breeding Double-crested Cormorants at two Wisconsin colonies. *Journal of Field Ornithology* 63:203-211.

- Custer, T.W., and R.G. Osborn. 1977. Feeding habitat use by colonially breeding herons, egrets, and ibises in North Carolina. *Auk* 95:733-743.
- Dorfman, E.J., and M.J. Kingsford. 2001. Environmental determinants of distribution and foraging behaviour of cormorants (*Phalacrocorax* spp.) in temperate estuarine habitats. *Marine Biology* 138:1-10.
- Dunn, E.H. 1975. Caloric intake of nestling Double-crested Cormorants. *Auk* 92:553-565.
- Emmett, R.L., S.L. Stone, S.A. Hinton, and M.E. Monaco. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Volume II: Species life history summaries. Estuarine Living Resources Report No. 8. National Oceanic and Atmospheric Administration/National Ocean Service, Strategic Environmental Assessments Division, Rockville, MD. 329 pp.
- Emmett, R., and R. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. *Northern Pacific Anadromous Fisheries Committee Bulletin* 2:11-20.
- Feltham, M.J. 1995. Consumption of Atlantic salmon smolts and parr by goosanders: Estimates from doubly-labelled water measurements of captive birds released on two Scottish rivers. *Journal of Fish Biology* 46:273-281.
- Fowle, M.R. 1997. Population dynamics, food habits, and bioenergetics of Double-crested Cormorants in Lake Champlain. M.S. thesis, University of Vermont, Burlington, VT.
- FPC (Fish Passage Center). 2002. Archived juvenile salmonid passage counts for 2000 and 2001. At <http://www.fpc.org/SMPDATA.html>.
- Furness, R.W., and T.R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655-656.
- Glahn, J.F., and R.B. McCoy. 1995. Measurements of wintering Double-crested Cormorants and discriminant models of sex. *Journal of Field Ornithology* 66:299-304.

- Gremillet, D., G. Argentin, B. Schulte, and B.M. Culik. 1998. Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: Benthic or pelagic feeding? *Ibis* 140:113-119.
- Haertel, L.S., and C.L. Osterberg. 1967. Ecology of zooplankton, benthos, and fishes in the Columbia River estuary. *Ecology* 48:459-472.
- Hatch, J.J., and D.V. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). In *The Birds of North America*, No. 441. A. Poole, and F. Gill (eds.), *The Birds of North America*, Inc., Philadelphia, PA.
- Hunt, G.L., Jr., R.W. Russell, K.O. Coyle, and T. Weingartner. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* 167: 241-259.
- Irons, D.B. 1982. Foraging strategies of Glaucous-winged Gulls: Influences of sea otter predation. M.S. thesis, Oregon State University, OR, USA. 76 pp.
- Irons, D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79:647:655.
- Ishikawa, K., and Y. Watanuki. 2002. Sex and individual differences in foraging behavior of Japanese Cormorants in years of different prey availability. *Journal of Ethology* 20:49-54.
- Jay, D.A., and J. D. Smith. 1990. Circulation, density distribution and neap-spring transitions in the Columbia River estuary. *Progress in Oceanography* 25:81-112.
- Jodice, P.G.R., R.B. Lanctot, V.A. Gill, D.D. Roby, and S.A. Hatch. 2000. Sexing adult Black-legged Kittiwakes by DNA, behavior, and morphology. *Waterbirds* 23:407-417.
- Johnsgard, P.A. 1993. *Cormorants, darters and pelicans of the world*. Smithsonian Institution Press, Washington, DC. 445 pp.
- Jones, K.K., C.A. Simenstad, D.L. Higley, and D.L. Bottom. 1990. Community structure, distribution, and standing stock of benthos, epibenthos, and plankton in the Columbia River estuary. *Progress in Oceanography* 25:211-241.

- Kato, A., I. Nishiumi, and Y. Naito. 1996. Sexual differences in diet of King Cormorants at Macquarie Island. *Polar Biology* 16:75-77.
- Kato, A., Y. Watanuki, P. Shaughnessy, Y. Le Maho, and Y. Naito. 1999. Intersexual differences in the diving behaviour of foraging Subantarctic Cormorant (*Phalacrocorax albiventer*) and Japanese Cormorant (*P. filamentosus*). *Physiology* 322:557-562.
- Kato, A., Y. Watanuki, I. Nishiumi, M. Kuroki, P. Shaughnessy, and Y. Naito. 2000. Variation in foraging and parental behaviour of King Cormorants. *Auk* 117:718-730.
- Kenward, R.E. 1992. Quantity versus quality: Programmed collection and analysis of radio-tracking data. Pages 231-246 *in* Priede, I.G. and S.M. Swift (eds.), *Wildlife telemetry remote monitoring and tracking of animals*. Ellis Horwood Ltd., New York, NY.
- Keuhl, R. O. 2000. Design of experiments: Statistical principles of research design and analysis, 2nd edition, Chapter 15. Brooks/Cole, Pacific Grove, CA. 666 pp.
- Krebs, J.R. 1978. Optimal foraging: Decision rules for predators. Pages 23-63 *in* Krebs, J.R., and N.B. Davies (eds.), *Behavioural ecology: An evolutionary approach*. Blackwell Scientific Pub., London, UK. 494 pp.
- Mauer, B. A. 1996. Energetics of avian foraging. Pages 250-279 *in* Carey, C. (ed.), *Avian energetics and nutritional ecology*. Chapman & Hall, New York, NY. 543 pp.
- Mendall, H.L. 1936. The home-life and economic status of the Double-crested Cormorant, *Phalacrocorax auritus auritus* (Lesson). University of Maine Studies, Second Series, no. 38. *Maine Bull.* 39.3. University Press, Orono, ME.
- Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. Pages 217-266 *in* Furness, R.W., and J.J.D. Greenwood (eds). *Birds as monitors of environmental change*. Chapman and Hall, New York, NY.
- Montevecchi, W.A., and R.A. Myers. 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. *Sarsia* 80:313-322.

- Montevecchi, W.A., and D.K. Cairns. 2002. Episodic predation on post-smolt Atlantic Salmon (*Salmo salar*) by Northern Gannets (*Morus bassanus*). NPAFC Technical Report 4:48-50.
- Morrow, J.E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publ. Co., Anchorage, AK. 248 pp.
- NMFS (National Marine Fisheries Service). 2002. Endangered Species Act status of west coast salmonids. NMFS, Northwest Region, Portland, OR. At <http://www.nwr.noaa.gov>.
- Nettleship, D.N., and D.C. Duffy (eds.) 1995. The Double-crested Cormorant: Biology, Conservation, and Management. Colonial Waterbirds 18 (Special Publication 1):1-256.
- Orcutt, H.G. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallas). California Fish and Game Bulletin 78:1-64.
- Pennycuik, C.J. 1975. Mechanics of flight. Pages 5-17 in Farner, D.S., and J.R. King (eds.). Avian Biology, Vol. 5., Academic Press, New York, NY.
- Raffaelli, D., H. Richner, R. Summers, and S. Northcott. 1990. Tidal migrations in the flounder (*Platichthys flesus*). Marine Behavioural Physiology 16:249-260.
- Ramsey, F.L., and D.W. Schafer. 1997. The statistical sleuth: A course in methods of data analysis. Wadsworth Publ. Co., Belmont, California, USA. 742 pp.
- Reise, K. 1985. Tidal flat ecology: An experimental approach to species interactions. Springer-Verlag, Berlin. 191 pp.
- Richner, H. 1995. Wintering cormorants *Phalacrocorax carbo carbo* in the Ythan estuary, Scotland: Numerical and behavioural responses to fluctuating prey availability. Ardea 83:193-197.
- Roby, D. D., D. P. Craig, K. Collis, and S. L. Adamany. 1998. Avian predation on juvenile salmonids in the lower Columbia River. 1997 Annual Report of the Oregon Cooperative Fish and Wildlife Research Unit at Oregon State University to Bonneville Power Administration and U.S. Army Corps of Engineers, Portland, OR. 148 pp.

- SAS Institute Inc. 1999. SAS/STAT Software, Version 8. SAS Institute Inc., Cary, NC.
- Schreiber, R.W., and R.B. Clapp. 1987. Pelecaniform feeding ecology. Pages 173-188 *in* Seabirds: Feeding ecology and role in marine ecosystems. Cambridge University Press, New York, NY. 408 pp.
- Selander, R. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- Simenstad, C.A., L.F. Small, C.D. McIntire, D.A. Jay, and C. Sherwood. 1990. Columbia River estuary studies: An introduction to the estuary, a brief history, and prior studies. *Progress in Oceanography* 25:1-13.
- S-PLUS. 1999. S-plus 2000, Release 3. MathSoft, Inc., Seattle, WA.
- Suryan, R.M., D.B. Irons, M. Kaufman, J. Benson, P.G.R. Jodice, D.D. Roby, and E.D. Brown. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series* 236:273-287.
- Trapp, J.L., S.J. Lewis, and D.M. Pence. 1997. Double-crested Cormorant impacts on sport fish: Literature review, agency survey, and strategies. Pages 17-26 *in* M.E. Tobin (ed.), Symposium on Double-crested Cormorants: Population status and management issues in the Mid-west. USDA/APHIS Tech. Bull. No. 1879. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Washington, DC. 164 pp.
- Trinast, E.M. 1975. Tidal currents and *Acaria* distributions in Newport Bay, California. *Estuarine and Coastal Marine Science* 3:165-176.
- USNO (United States Naval Observatory). 2002. Sunrise/sunset and civil twilight tables for Astoria, Oregon in 2001. Astronomical Applications Department, Washington, DC. At <http://aa.usno.navy.mil/data/docs>.
- Van Eerden, M.R., and B. Voslamber. 1995. Mass fishing by Cormorants *Phalacrocorax carbo sinensis* at Lake IJsselmeer, the Netherlands: A recent and successful adaptation to a turbid environment. *Ardea* 83:199-212.

- van Tets, G.F. 1959. A comparative study of some social communication patterns in the Pelecaniformes. Ornithological Monograph No. 2: American Ornithologists' Union, Washington, DC.
- Voslamber, B., M. Platteeu, and M.R. Van Eerden. 1995. Solitary foraging in sand pits by breeding cormorants *Phalacrocorax carbo sinensis*: Does specialized knowledge about fishing sites and fish behaviour pay off? *Ardea* 83:213-222.
- Wanless, S., M.P. Harris, and J.A. Morris. 1995. Factors affecting daily activity budgets of South Georgian Shags during chick rearing at Bird Island, South Georgia. *Condor* 97:550-558.
- Watanuki, Y., A. Kato, and Y. Naito. 1996. Diving performance of male and female Japanese Cormorants. *Canadian Journal of Zoology* 74:1098-1109.
- Weimerskirch, H., O. Chastel, L. Ackermann, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeier, and J. Judas. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* 47:472-476.
- White, G.C., and R.A. Garrott. 1990. Analysis of Wildlife Radio-tracking Data. Academic Press, Inc., New York, NY. 383 pp.
- Whitfield, A.K., and S.J.M. Blaber. 1979. Feeding ecology of piscivorous birds at Lake St. Lucia. Part 3. Swimming Birds. *Ostrich* 50:10-20.
- Wirjoatmodjo, S., and T.J. Pitcher. 1984. Flounders follow the tides to feed: Evidence from ultrasonic tracking in an estuary. *Estuarine, Coastal and Shelf Science* 19:231-241.
- Wolff, W.J., M.A. Mardos, and A.J.J. Sandee. 1981. Tidal migration of plaice and flounders as a feeding strategy. Pages 159-171 *in* Jones, N.J., Wolff, W.J. (eds.), Feeding and survival strategies of estuarine organisms. Plenum Press, New York, NY. 304 pp.
- Zamon, J.E. 2000. The influence of tidal currents on plankton densities and energy flow to seals, seabirds, and schooling fishes in the San Juan Islands, Washington, USA. Ph.D. thesis, University of California, Irvine, CA. 181 pp.

Table 1.3. Poisson log-linear regression model for factors affecting the productivity of Double-crested Cormorant nests during the 2001 nesting season.

	Coefficient	Standard Error	<i>F</i>	<i>P</i>
Constant	0.4873	1.169	0.17	0.677
<i>Sub-colony</i>	-0.5371	0.1828	8.57	0.004
<i>Nearest neighbour distance</i>	0.0027	0.0041	0.44	0.511
<i>Distance from gull habitat</i>	0.0012	0.0005	5.18	0.025
<i>Nest elevation</i>	-0.0003	0.0023	0.02	0.884
<i>Initiation date</i>	0.0010	0.0084	0.02	0.902
Deviance = 69.74 d.f. = 119				

Table 2.2. Separate split-plot-in-time ANOVAs for each factorial effect of time of day, tide stage, and tide series on the proportion of time actively-nesting Double-crested Cormorants spent off-colony (presumably foraging) during June of 2001. Error terms are shown in italics below each set of factorial effects.

Effect	d.f.	Mean Square	Sum of Squares	<i>F</i>	<i>P</i>
sex	1	0.3433	0.3433	4.11	0.0517
	30	<i>0.0836</i>	<i>2.5087</i>		
daytime	2	1.1583	2.3165	27.19	<0.0001
sex*daytime	2	0.0372	0.0743	0.87	0.4235
	60	<i>0.0426</i>	<i>2.5581</i>		
tide stage	1	0.3921	0.3921	34.77	<0.0001
sex*tide stage	1	0.0006	0.0006	0.05	0.8224
	30	<i>0.0113</i>	<i>0.3381</i>		
tide series	1	0.0645	0.0645	2.78	0.1058
sex*tide series	1	0.0205	0.0205	0.88	0.3553
	30	<i>0.0233</i>	<i>0.6982</i>		
daytime*tide stage	2	0.2289	0.4579	13.65	<0.0001
sex*daytime*tide stage	2	0.0083	0.0166	0.49	0.6121
	60	<i>0.0168</i>	<i>1.0071</i>		
daytime*tide series	2	0.0411	0.0821	2.54	0.0876
sex*daytime*tide series	2	0.0008	0.0016	0.05	0.9525
	60	<i>0.0162</i>	<i>0.9715</i>		
tide stage*tide series	1	0.0060	0.0060	0.45	0.5058
sex*tide stage*tide series	1	0.0053	0.0053	0.40	0.5300
	30	<i>0.0131</i>	<i>0.3917</i>		
daytime*stage*series	2	1.1806	2.3611	56.69	<0.0001
sex*daytime*stage*series	2	0.0182	0.0364	0.92	0.4042
<i>residual</i>	60	<i>0.0198</i>	<i>1.1867</i>		

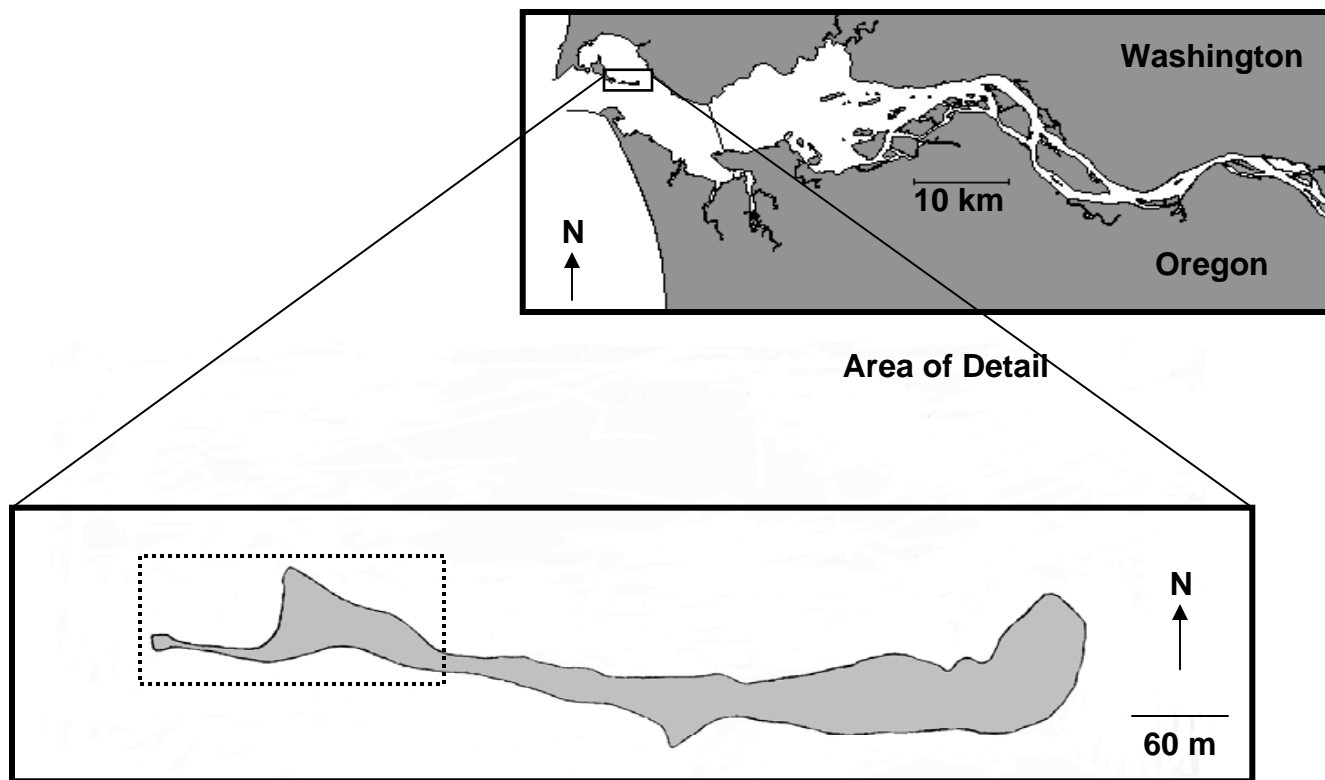


Figure 1.1. Map of study area (dotted rectangle) on the west end of East Sand Island in Clatsop County, Oregon in the Columbia River estuary.

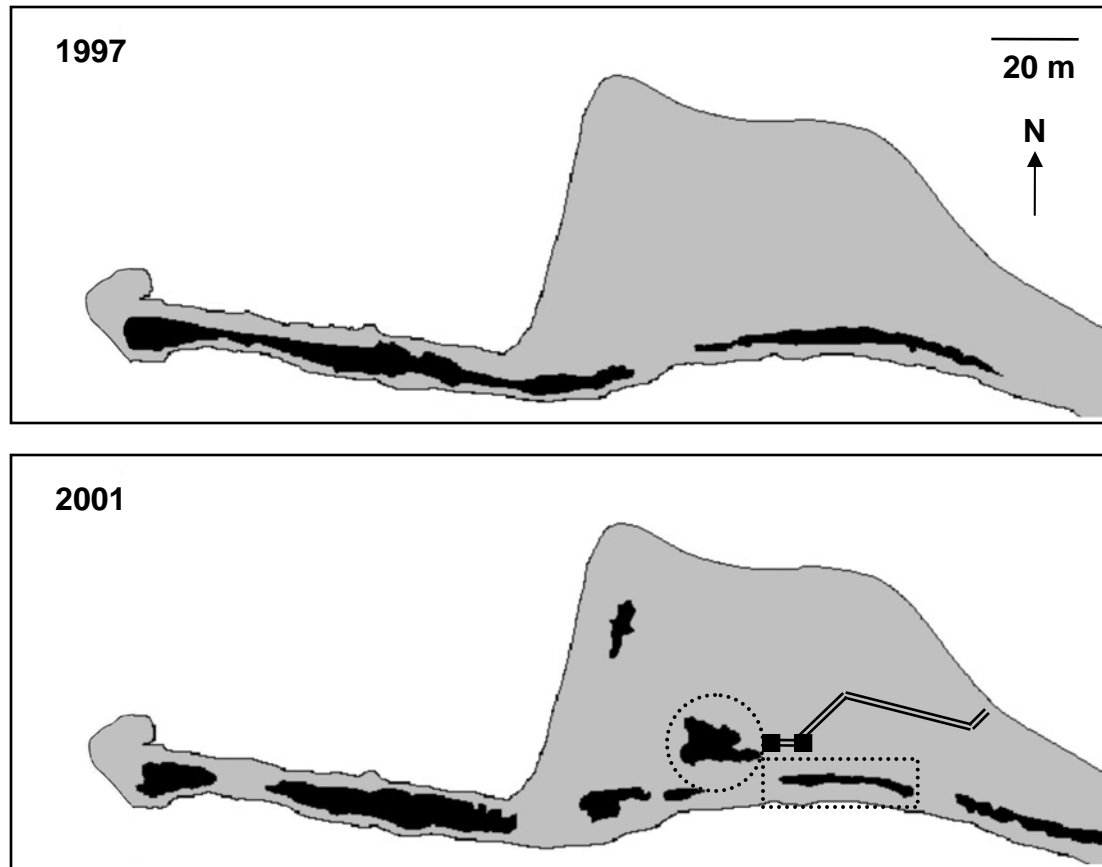


Figure 1.2. Locations of sub-colonies (black polygons) of nesting Double-crested Cormorants on the west end of East Sand Island (shown in gray) during 1997 (above) and 2001 (below). Schematics are based on aerial photographs taken during mid-incubation each year. The satellite sub-colony (dotted circle) and the main sub-colony (dotted rectangle), observation blinds (black squares), and above-ground tunnel system (double-lines) are also shown.

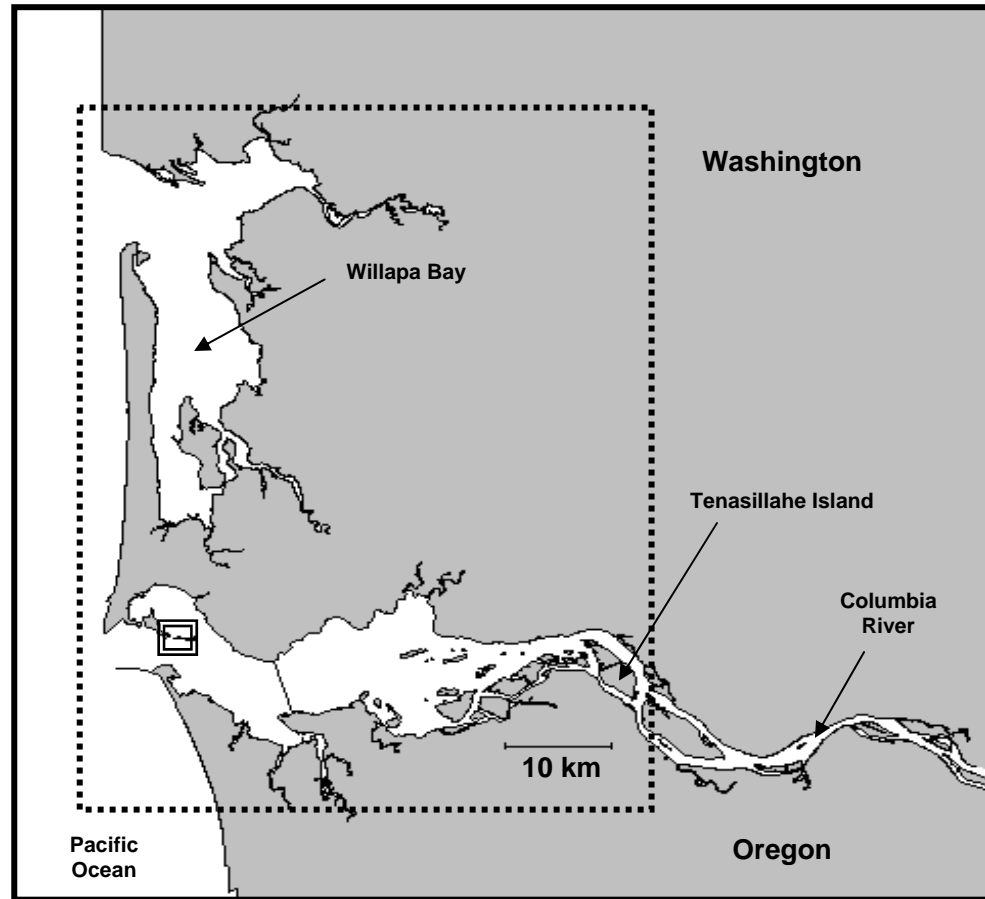


Figure 2.1. Map of the study area indicating the aerial telemetry survey area (dotted rectangle) searched for foraging radio-tagged Double-crested Cormorants nesting on East Sand Island (double-lined square) in the Columbia River estuary.

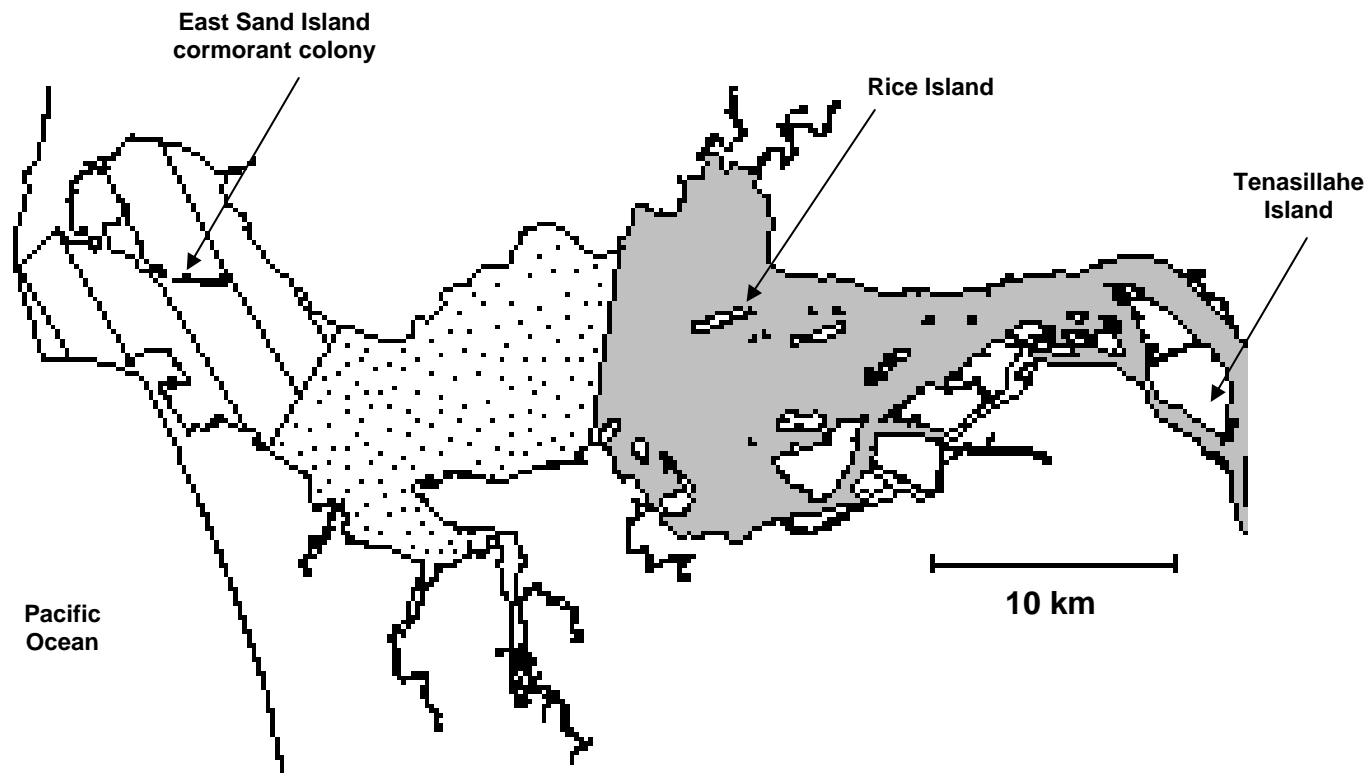


Figure 2.2. Salinity gradient for the Columbia River estuary, showing marine zone (stripes), estuarine-mixing zone (dotted), and freshwater zone (gray) (defined by Simenstad et al. 1990).



Figure 2.3. Aerial telemetry detections of male (cross, $N = 125$) and female (circle, $N = 61$) Double-crested Cormorants actively-nesting on East Sand Island (double-lined rectangle). Surveys were conducted throughout the Columbia River estuary between 1 June and 26 July, in 2000 ($N = 138$ relocations) and 2001 ($N = 48$ relocations).

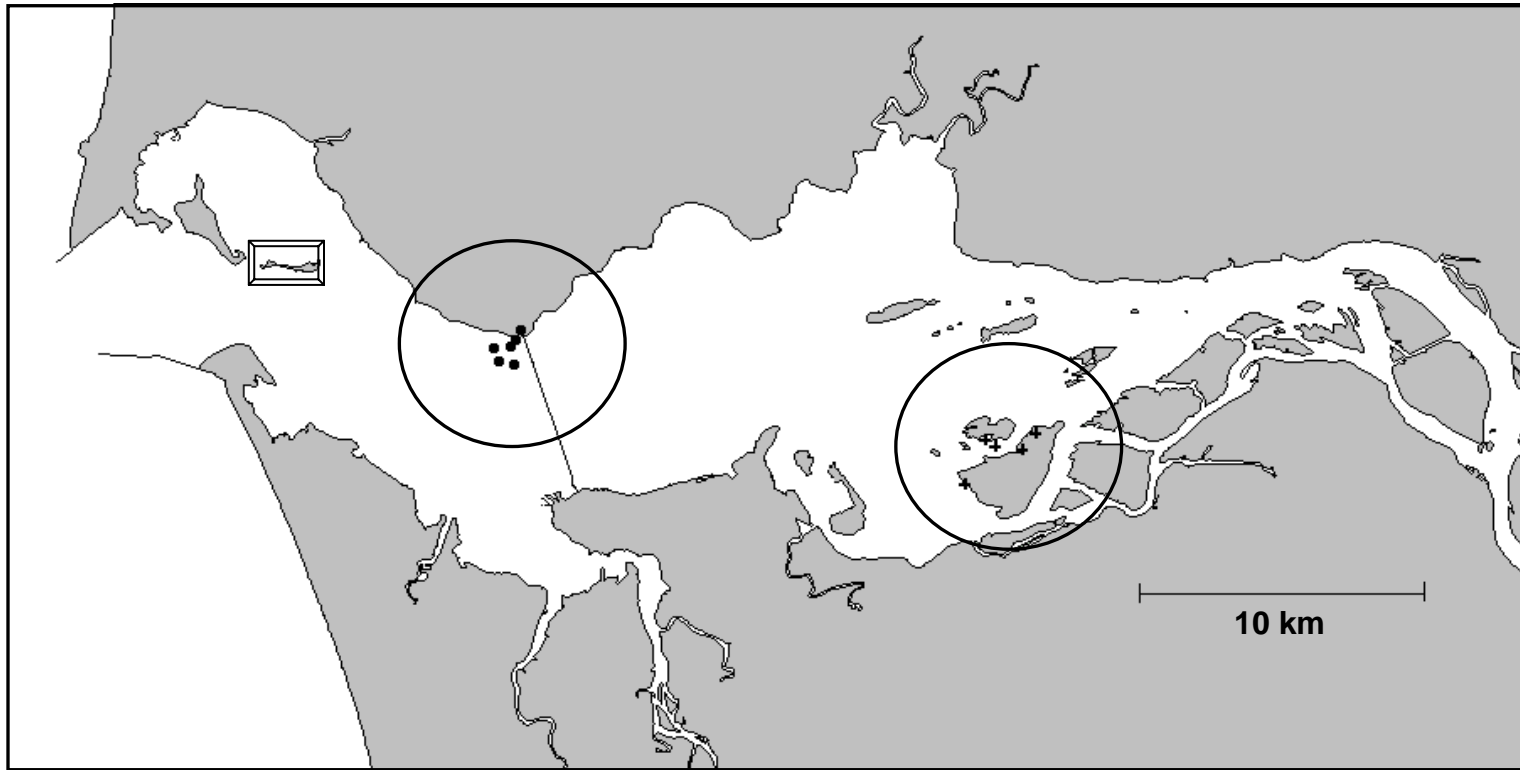
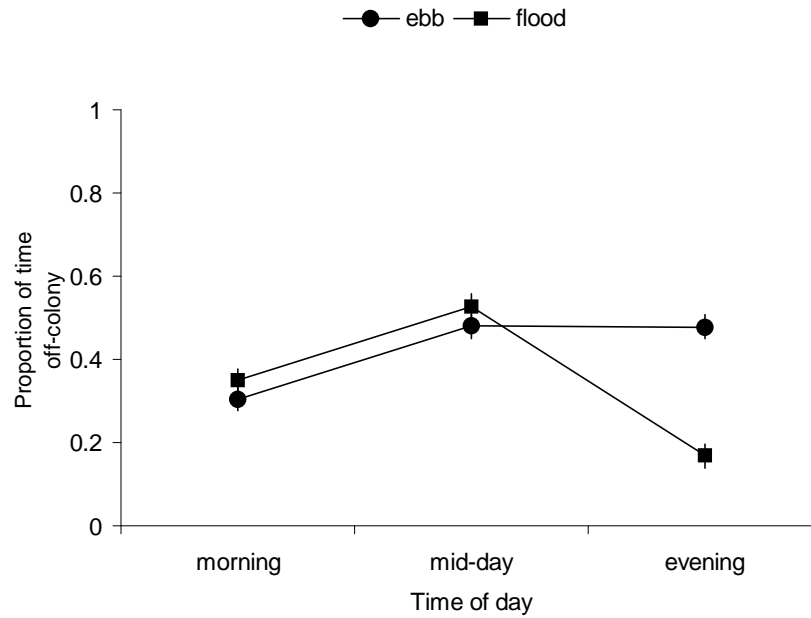


Figure 2.5. Distribution of aerial telemetry relocations for two individual radio-tagged Double-crested Cormorants (6 relocations for one female shown as solid circles and 5 relocations for one male shown as crosses) actively-nesting at East Sand Island (double-lined rectangle) in the Columbia River estuary.

A. NEAP



B. SPRING

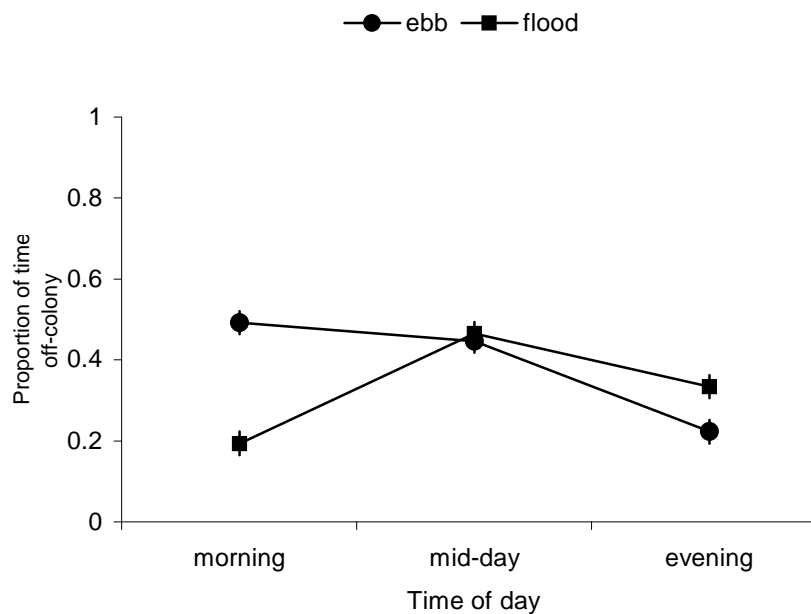


Figure 2.6. Proportion of time spent off-colony (and presumably foraging) in June of 2001 for radio-tagged Double-crested Cormorants actively-nesting on East Sand Island during neap (A) and spring (B) tide series by time of day and tide stage. Proportion of time off-colony is expressed as the proportion of detection cycles when a transmitter was not detected for at least 2 consecutive scanning cycles by on-colony receiving stations for each combination of time of day, tide stage, and tidal series.

CHAPTER 4

SYNOPSIS AND CONCLUSIONS

Food availability within the Columbia River estuary appears to be intricately linked to colony size, reproductive success, and foraging patterns of Double-crested Cormorants nesting at East Sand Island. We speculate that food resources are more stable and predictable in the Columbia River estuary compared to coastal and interior nesting areas that are likely influenced to a greater extent by fluctuating oceanic and climatic conditions. The more predictable food resources in the Columbia River estuary, including local forage fish stocks and salmonid smolts, likely makes East Sand Island an appealing nesting site for prospecting adult Double-crested Cormorants. Immigration has played a key role in the dramatic increases in numbers of nesting cormorants at the East Sand Island colony, likely due to recruitment of breeding adults that emigrated from colonies in interior Oregon, and from coastal colonies in Washington and British Columbia, especially during years of poor ocean conditions.

The high reproductive success of cormorants nesting in a newly-established satellite sub-colony suggests that considerable quality habitat remains for expansion and/or establishment of new satellite sub-colonies on East Sand Island. We predict that the East Sand Island cormorant colony will continue to expand into available nesting habitat during years of high forage fish availability. During years of low forage fish availability

(i.e., El Niño years), however, reproductive success at the colony on East Sand Island may suffer significant declines for two major reasons. First, depredation by nesting gulls following Bald Eagle disturbances will likely increase when forage fish are less available as a primary food source. Second, prey resources near the colony may become limited and/or depleted due to competition for food with thousands of other piscivorous waterbirds. For these reasons, declines in reproductive performance may result in reduced recruitment to the colony and, consequently, limit colony size.

During the years of my study, marine forage fish were comparatively abundant in the Columbia River estuary and there was little evidence that intraspecific competition for food resources near the colony was limiting reproductive performance of Double-crested Cormorants in a density-dependent manner. There was strong evidence, however, that cormorants were commuting considerable distances to forage in the estuarine-mixing and freshwater zones of the estuary where fish resources were apparently more available and, perhaps, to avoid intraspecific and interspecific competition for food in close proximity to the colony. We speculate that in years when ocean conditions are poor and stocks of marine forage fishes are low within the estuary that nesting Double-crested Cormorants may become more reliant on the more predictable fish resources of the estuary, such as the millions of hatchery-reared salmonid smolts that are released annually. Marked gender

differences in foraging distribution and the ability to forage over a large area on a wide variety of prey may be critical for this large and growing colony of cormorants to remain productive when forage fish stocks become more limited and competition with many thousands of other nesting and roosting piscivorous waterbirds becomes more stringent.

Future directions

Direct observations of the foraging behaviour of marked cormorants would contribute to our understanding of how individuals locate and capture prey. A few questions of particular interest are:

1. Do cormorants employ different foraging strategies to capture schooling vs. demersal prey?
2. Do cormorant foraging behaviours change with tidal currents, turbidity, and/or habitat?
3. Do cormorant foraging behaviours change during peak out-migration of salmonid smolts?
4. How do cormorants alter their foraging distribution and foraging patterns during years of poor ocean conditions and low availability of marine forage fishes?
5. How do the foraging strategies employed by the cormorants nesting on East Sand Island compare to Double-crested Cormorants nesting in other estuarine environments (i.e., smaller estuaries, rivers with natural river flow)?

An assessment of the health status (e.g., physiological condition, parasite and contaminant burdens) of breeding adults and nestlings at the East Sand Island colony would provide baseline information to monitor the overall health of this large cormorant colony. These data may reveal underlying health problems within the colony and/or permit early detection of the presence of various contagious diseases (e.g., Newcastle disease) or toxicant effects.

Continued monitoring of the numbers and productivity of Double-crested Cormorants nesting at the East Sand Island colony is warranted as this colony represents a substantial proportion (>40%) of the West Coast population. Furthermore, data on colony size and productivity are needed from throughout the range of the West Coast subspecies of Double-crested Cormorant. Data collected in a consistent manner are necessary to begin to understand the extent to which factors limiting the size and reproductive success of the East Sand Island colony are also influencing population trends of Double-crested Cormorants throughout the Pacific Coast of North America.

BIBLIOGRAPHY

- Aebischer, N.J. 1986. Retrospective investigation of an ecological disaster in the Shag, *Phalacrocorax aristotelis*: A general method based on long-term marking. *Journal of Animal Ecology* 55:613-629.
- Ainley, D.G., and R.J. Boekelheide (eds.). 1990. *Seabirds of the Farallon Islands*. Stanford University Press, Stanford, CA. 450 pp.
- Allredge, A.L., and W.M. Hamner. 1980. Recurring aggregation of zooplankton by a tidal current. *Estuarine and Coastal Marine Science* 10:31-37.
- Anderson, D.J., and P.J. Hodum. 1993. Predator behavior favors clumped nesting in an oceanic seabird. *Ecology* 74:2462-2464.
- Anderson, D.J., and R.E. Ricklefs. 1987. Radio-tracking Masked and Blue-footed Boobies (*Sula* spp.) in the Galapagos Islands. *National Geographic Research* 3:152-163.
- Andrews, D.J., and K.R. Day. 1999. Reproductive success in the Great Cormorant *Phalacrocorax carbo carbo* in relation to colony nest position and timing of nesting. *Atlantic Seabirds* 1:107-120.
- Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-473.
- Ballard, G., D.G. Ainley, C.A. Ribic, and K.R. Barton. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adelie Penguins. *Condor* 103:481-490.
- Bayer, R.D. 1986. Seabirds near an Oregon estuarine salmon hatchery in 1982 and during the 1983 El Niño. *Fishery Bulletin* 84:279-286.
- Bernstein, N.P., and S.J. Maxson. 1984. Sexually distinct daily activity patterns of Blue-eyed Shags in Antarctica. *Condor* 86:151-156.
- Birkhead, T.R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). *Journal of Animal Ecology* 46:751-764.
- Birkhead, T.R., and R.W. Furness. 1985. The regulation of seabird populations. Pages 145-167 in Sibly, R.M., and R.H. Smith (eds.), *Behavioural Ecology*. Blackwell, Oxford.

- Birt, V.L., T.P. Birt, D. Goulet, D.K. Cairns, and W.A. Montevecchi. 1987. Ashmole's halo: Direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40:205-208.
- Blackwell, B.F., W.B. Krohn, N.R. Dube, and A.J. Godin. 1997. Spring prey use by Double-crested Cormorants on the Penobscot River, Maine, USA. *Colonial Waterbirds* 20:77-86.
- Boots, B., and A. Getis. 1978. Point pattern analysis. Sage Publications, London, UK. 93 pp.
- Bottom, D.L., K.K. Jones, and M.J. Herring. 1984. Fishes of the Columbia River estuary. Final report on the Fish Work unit of the Columbia River Estuary Data Development Program. Oregon Department of Fish and Wildlife, Corvallis, OR. 113 pp.
- Bottom, D.L., and K.K. Jones. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. *Progress in Oceanography* 25:243-270.
- Boulinier, T., and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology* 11:505-517.
- Brodeur, R., W.G. Pearcy, and S. Ralston. *In review*. Abundance and distribution patterns of nekton and micronekton in the Northern California current transition zone. *Journal of Oceanography*.
- Broley, C.L. 1947. Migration and nesting of Florida Bald Eagles. *Wilson Bulletin* 59:1-68.
- Brunton, D.H. 1977. Impacts of predators: Center nests are less successful than edge nests in a large nesting colony of Least Terns. *Condor* 99:372-380.
- Cairns, D.K. 1992. Population regulation of seabird colonies. Pages 37-61 *in* D.M. Power (ed.), *Current ornithology*. Vol. 9. Plenum, New York, NY.
- Cairns, D.K., R.L. Dibblee, and P.-Y. Daoust. 1998. Displacement of a large Double-crested Cormorant, *Phalacrocorax auritus*, colony following human disturbance. *Canadian Field-Naturalist* 112:520-522.

- Campbell, R.W. 1969. Bald Eagle swimming in ocean with prey. *Auk* 86:561.
- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. 1990. The birds of British Columbia. Vol.1. Nonpasserines: loons through waterfowl. Royal British Columbia Museum, Victoria, and Canadian Wildlife Service, Delta, BC. 535 pp.
- Cannings, R.J. 1998. The birds of British Columbia – a taxonomic catalogue. British Columbia Ministry of the Environment, Lands and Parks, Wildlife Branch, Victoria, BC. Wildlife Bulletin No. B-86. 252 pp.
- Carey, C. 1996. Female reproductive energetics. Pages 324-374 *in* Carey, C. (ed.), *Avian energetics and nutritional ecology*. Chapman & Hall, New York, NY. 543 pp.
- Carter, H.R., A.L. Sowls, M.S. Rodway, U.W. Wilson, R.W. Lowe, G.J. McChesney, F. Gress, and D.L. Anderson. 1995. Population size, trends, and conservation problems of the Double-crested Cormorant on the Pacific Coast of North America. *Colonial Waterbirds* 18 (Special Publication 1):189-215.
- Casaux, R., M. Favero, P. Silva, and A. Baroni. 2001. Sex differences in the diving depths and diet of Antarctic Shags at the South Shetland Islands. *Journal of Field Ornithology* 72:22-29.
- Caswell, H. 2001. *Matrix population models: Construction, analysis and interpretation*, 2nd ed. Sinauer Assoc., Inc., Sunderland, MA. 722 pp.
- Clode, D. 1993. Colonially breeding seabirds: Predators or prey? *Trends in Ecology and Evolution* 8:336-338.
- Collis, K., S.L. Adamany, D.D. Roby, D.P. Craig, and D.E. Lyons. 1999. 1998 Annual Report of the Oregon Cooperative Fish and Wildlife Research Unit to Bonneville Power Administration and the U.S. Army Corps of Engineers, Portland, OR. 148 pp.
- Collis, K., M. Hawbecker, D.D. Roby, C. Couch, J. Wolf, and C.D. Anderson. 2001. Pelican, cormorant, and pinniped use of pile dikes and jetties at the mouth of the Columbia River estuary, 2000. Unpublished report, Oregon State University, Corvallis, OR. 39 pp.

- Collis, K., D.D. Roby, D.P. Craig, S.L. Adamany, J.Y. Adkins, and D.E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537-550.
- Conservation Data Centre. 2002. RED and BLUE LISTS for British Columbia amphibians, reptiles, birds, and mammals. At <http://srmwww.gov.bc.ca/cdc/tracking.htm>.
- CO-OPS (Center for Operational Oceanographic Products and Services). 2002. Hourly water level predictions for Astoria, OR, 2000 and 2001. NOAA, NOS. At <http://co-ops.nos.noaa.gov>
- Coulson, J.C. 1968. Differences in the quality of birds nesting in the center and on the edge of a colony. *Nature* 217:211-227.
- Craven, S.R., and E. Lev. 1987. Double-crested Cormorants in the Apostle Islands, Wisconsin, USA: Population trends, food habits and fishery deprecations. *Colonial Waterbirds* 10:64-71.
- Custer, T.W., and C. Bunck. 1992. Feeding flights of breeding Double-crested Cormorants at two Wisconsin colonies. *Journal of Field Ornithology* 63:203-211.
- Custer, T.W., and R.G. Osborn. 1977. Feeding habitat use by colonially breeding herons, egrets, and ibises in North Carolina. *Auk* 95:733-743.
- Danchin, E., and R.H. Wagner. 1997. The evolution of coloniality: The emergence of new perspectives. *Trends in Ecology and Evolution* 14:405-410.
- Danchin, E., T. Boulinier, and M. Massot. 1998. Breeding habitat selection based on conspecific reproductive success: Implications for the evolution of coloniality. *Ecology* 79:2415-2428.
- DesGranges, J.L., and A. Reed. 1981. Disturbance and control of selected colonies of Double-crested Cormorants in Quebec. *Colonial Waterbirds* 4:12-19.
- Dorfman, E.J., and M.J. Kingsford. 2001. Environmental determinants of distribution and foraging behaviour of cormorants (*Phalacrocorax* spp.) in temperate estuarine habitats. *Marine Biology* 138:1-10.

- Dunn, E.H. 1975. Caloric intake of nestling Double-crested Cormorants. *Auk* 92:553-565.
- Emmett, R.L., S.L. Stone, S.A. Hinton, and M.E. Monaco. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Volume II: Species life history summaries. Estuarine Living Resources Report No. 8. National Oceanic and Atmospheric Administration/National Ocean Service, Strategic Environmental Assessments Division, Rockville, MD. 329 pp.
- Emmett, R., and R. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. *North Pacific Anadromous Fish Commission Bulletin* 2:11-20.
- Feltham, M.J. 1995. Consumption of Atlantic salmon smolts and parr by goosanders: Estimates from doubly-labelled water measurements of captive birds released on two Scottish rivers. *Journal of Fish Biology* 46:273-281.
- Fowle, M.R. 1997. Population dynamics, food habits, and bioenergetics of Double-crested Cormorants in Lake Champlain. M.S. thesis, University of Vermont, Burlington, VT.
- FPC (Fish Passage Center). 2002. Archived juvenile salmonid passage counts for 2000 and 2001. At <http://www.fpc.org/SMPDATA.html>.
- Furness, R.W. 1984. Influences of adult age and experience, nest location, clutch size and laying sequence on the breeding success of the Great Skua *Catharacta skua*. *Journal of Zoology (London)* 202:565-576.
- Furness, R.W., and T.R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655-656.
- Furness, R.W., and P. Monaghan. 1987. *Seabird ecology*. Blackie, Oxford. 164 pp.
- Garrett, M., R.G. Anthony, J.W. Watson, and K. McGarigal. 1988. Ecology of Bald Eagles on the lower Columbia River. Report to the United States Army Corps of Engineers, Portland, OR. 191 pp.

- Gaston, A.J., G. Chapdelaine, and D.G. Noble. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: Inter- and intra-colony variation. *Canadian Journal of Zoology* 61:2465-2475.
- Gaston, A.J., and G.E.J. Smith. 1984. The interpretation of aerial surveys for seabirds: Some effects of behaviour. *Canadian Wildlife Service Occasional Paper* 53:1-20.
- Glahn, J.F., and R.B. McCoy. 1995. Measurements of wintering Double-crested Cormorants and discriminant models of sex. *Journal of Field Ornithology* 66:299-304.
- Good, T.P. 2002. Breeding success in the Western Gull X Glaucous-winged Gull complex: The influence of habitat and nest-site characteristics. *Condor* 104:353-365.
- Gremillet, D., G. Argentin, B. Schulte, and B.M. Culik. 1998. Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: Benthic or pelagic feeding? *Ibis* 140:113-119.
- Haertel, L.S., and C.L. Osterberg. 1967. Ecology of zooplankton, benthos, and fishes in the Columbia River estuary. *Ecology* 48:459-472.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:142-159.
- Hatch, J.J. 1995. Changing populations of Double-crested Cormorants. *Colonial Waterbirds* 18 (Special Publication 1):8-24.
- Hatch, J.J., and D.V. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). In *The Birds of North America*, No. 441 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA. 36 pp.
- Hatchwell, B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*). *Journal of Animal Ecology* 60:721-736.
- Henny, C.J., L.J. Blus, S.P. Thompson, and U.W. Wilson. 1989. Environmental contaminants, human disturbance and nesting of Double-crested Cormorants in Northwestern Washington. *Colonial Waterbirds* 12:198-206.

- Hobson, K.A., R.W. Knapton, and W. Lysack. 1989. Population, diet and reproductive success of Double-crested Cormorants breeding on Lake Winnipegosis, Manitoba, in 1987. *Colonial Waterbirds* 12:191-197.
- Hodder, J., and M.R. Graybill. 1985. Reproduction and survival of seabirds in Oregon during the 1982-1983 El Niño. *Condor* 87:535-541.
- Hunt, G.L. Jr., Z.A. Eppley, and D.C. Schneider. 1986. Reproductive performance of seabirds: The importance of population and colony size. *Auk* 103:306-317.
- Hunt, G.L., Jr., R.W. Russell, K.O. Coyle, and T. Weingartner. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* 167: 241-259.
- Hunt, W.G., R.E. Jackman, J.M. Jenkins, C.G. Thelander, and R.E. Lehman. 1992. Northward post-fledging migration of California Bald Eagles. *Journal of Raptor Research* 25:19-23.
- Irons, D.B. 1982. Foraging strategies of Glaucous-winged Gulls: Influences of sea otter predation. M.S. thesis, Oregon State University, OR, USA. 76 pp.
- Irons, D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79:647:655.
- Isaacs, F.B., and R.G. Anthony. 2002. Bald Eagle nest locations and history of use in Oregon and the Washington portion of the Columbia River Recovery Zone, 1971 through 2001. Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR. 33 pp.
- Isaacs, F.B., R.G. Anthony, and R. J. Anderson. 1983. Distribution and productivity of nesting Bald Eagles in Oregon 1978-1982. *Murrelet* 64:33- 38.
- Ishikawa, K., and Y. Watanuki. 2002. Sex and individual differences in foraging behavior of Japanese Cormorants in years of different prey availability. *Journal of Ethology* 20:49-54.
- Jackman, R.E., W.G. Hunt, J.M. Jenkins, and P.J. Detrich. 1999. Prey of nesting Bald Eagles in northern California. *Journal of Raptor Research* 33:87-96.

- Jay, D.A., and J. D. Smith. 1990. Circulation, density distribution and neap-spring transitions in the Columbia River estuary. *Progress in Oceanography* 25:81-112.
- Jenkins, J.M., R.E. Jackman, and W.G. Hunt. 1999. Survival and movements of immature Bald Eagles fledged in northern California. *Journal of Raptor Research* 33:81-86.
- Jodice, P.G.R., R.B. Lanctot, V.A. Gill, D.D. Roby, and S.A. Hatch. 2000. Sexing adult Black-legged Kittiwakes by DNA, behavior, and morphology. *Waterbirds* 23:407-417.
- Johnsgard, P.A. 1993. *Cormorants, darters and pelicans of the world*. Smithsonian Institution Press, Washington, DC. 445 pp.
- Jones, K.K., C.A. Simenstad, D.L. Higley, and D.L. Bottom. 1990. Community structure, distribution, and standing stock of benthos, epibenthos, and plankton in the Columbia River estuary. *Progress in Oceanography* 25:211-241.
- Kato, A., I. Nishiumi, and Y. Naito. 1996. Sexual differences in diet of King Cormorants at Macquarie Island. *Polar Biology* 16:75-77.
- Kato, A., Y. Watanuki, P. Shaughnessy, Y. Le Maho, and Y. Naito. 1999. Intersexual differences in the diving behaviour of foraging Subantarctic Cormorant (*Phalacrocorax albiventer*) and Japanese Cormorant (*P. filamentosus*). *Physiology* 322:557-562.
- Kato, A., Y. Watanuki, I. Nishiumi, M. Kuroki, P. Shaughnessy, and Y. Naito. 2000. Variation in foraging and parental behaviour of King Cormorants. *Auk* 117:718-730.
- Kenward, R.E. 1992. Quantity versus quality: Programmed collection and analysis of radio-tracking data. Pages 231-246 *in* Priede, I.G. and S.M. Swift (eds.), *Wildlife telemetry remote monitoring and tracking of animals*. Ellis Horwood Ltd., New York, NY.
- Keuhl, R. O. 2000 *Design of experiments: Statistical principles of research design and analysis*, 2nd edition, Chapter 15. Brooks/Cole, Pacific Grove, CA. 666 pp.
- Krebs, J.R. 1978. Optimal foraging: Decision rules for predators. Pages 23-63 *in* Krebs, J.R., and N.B. Davies (eds.), *Behavioural ecology: An evolutionary approach*. Blackwell Scientific Pub., London, UK. 494 pp.

- Kruuk, H. 1964. Predators and antipredator behaviour of the Black-headed Gull (*Larus ridibundus*). Behaviour, Supplement 11:1-129.
- Kury, C.R., and M. Gochfeld. 1975. Human interference and gull predation in cormorant colonies. Biological Conservation 8:23-34.
- Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Proceedings of the International Ornithological Congress 14:30-42.
- Léger, C., and R. McNeil. 1987. Choix de l'emplacement des nids de Cormorans à Aigrettes (*Phalacrocorax auritus*) aux îles de la Madeleine, Québec. Canadian Journal of Zoology 65:24-34.
- Lewis, H.F. 1929. The natural history of the Double-crested Cormorant (*Phalacrocorax auritus auritus* (Lesson)). Ru-Mi-Lou Books, Ottawa, ON. 94 pp.
- Mauer, B. A. 1996. Energetics of avian foraging. Pages 250-279 in Carey, C. (ed.), Avian energetics and nutritional ecology. Chapman & Hall, New York, NY. 543 pp.
- McCullagh, P., and J.A. Nelder. 1989. Generalized Linear Models, 2nd ed. Chapman & Hall, London, UK. 511 pp.
- McGarigal, K., R.G. Anthony, and F.B. Isaacs. 1991. Interactions of humans and Bald Eagles on the Columbia River estuary. Wildlife Monographs, No.115. The Wildlife Society, Inc. 47 pp.
- McNeil, R., and C. Léger. 1987. Nest-quality and reproductive success of early- and late-nesting Double-crested Cormorants. Wilson Bulletin 99:262-267.
- Mendall, H.L. 1936. The home-life and economic status of the Double-crested Cormorant, *Phalacrocorax auritus auritus* (Lesson). University of Maine Studies, Second Series, no. 38. Maine Bull. 39.3. University Press, Orono, MN.
- Mitchell, R.M. 1977. Breeding biology of the Double-crested Cormorant on Utah Lake. Great Basin Naturalist 37:1-23.
- Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. Pages 217-266 in Furness, R.W., and J.J.D. Greenwood (eds). Birds as monitors of environmental change. Chapman and Hall, New York, NY.

- Montevecchi, W.A., and R.A. Myers. 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. *Sarsia* 80:313-322.
- Montevecchi, W.A., and D.K. Cairns. 2002. Episodic predation on post-smolt Atlantic Salmon (*Salmo salar*) by Northern Gannets (*Morus bassanus*). NPAFC Technical Report 4:48-50.
- Morrow, J.E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publ. Co., Anchorage, AK. 248 pp.
- Moul, I.E. 1996. Seasonal movement patterns of Double-crested Cormorants in the Strait of Georgia and Puget Sound 1994-1996. Unpublished report. Canadian Wildlife Service, Pacific Wildlife Research Centre, Delta, BC. 111 pp.
- Moul, I.E. 2000. Population trends of Double-crested and Pelagic cormorants nesting along the southern coast of Vancouver Island, 1999. Unpublished report, British Columbia Ministry of the Environment, Lands and Parks, Nanaimo, BC. 21 pp.
- Moul, I.E., and M.B. Gebauer. 2002. Status of the Double-crested Cormorant in British Columbia. British Columbia Ministry of Water, Land, and Air Protection, Biodiversity Branch, Victoria, BC. Wildlife Working Report No. WR-105. 36 pp.
- NMFS (National Marine Fisheries Service). 2002. Endangered Species Act status of west coast salmonids. NMFS, Northwest Region, Portland, OR. At <http://www.nwr.noaa.gov>.
- Nettleship, D.N., and D.C. Duffy (eds.). 1995. The Double-crested Cormorant: Biology, Conservation, and Management. *Colonial Waterbirds* 18 (Special Publication 1):1-256.
- Orcutt, H.G. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallas). *California Fish and Game Bulletin* 78:1-64.
- Paine, R.T., J.T. Wootton, and P.D. Boersma. 1990. Direct and indirect effects of Peregrine Falcon predation on seabird abundance. *Auk* 107:1-9.
- Palacios, E., and E. Mellink. 2000. Nesting waterbirds on Isla San Martin and Todos Santos, Baja California. *Western Birds* 31:184-189.
- Parrish, J.K. 1995. Influence of group size and habitat type on reproductive success in Common Murres (*Uria aalge*). *Auk* 112:390-401.

- Parrish, J.K., M. Marvier, and R.T. Paine. 2001. Direct and indirect effects: Interactions between Bald Eagles and Common Murres. *Ecological Applications* 11:1858-1869.
- Pennycuik, C.J. 1975. Mechanics of flight. Pages 5-17 *in* Farner, D.S., and J.R. King (eds.). *Avian Biology*, Vol. 5., Academic Press, New York, NY.
- Peters, C.F., K.O. Richter, D.A. Manuwal, and S.G. Herman. 1978. Colonial nesting sea and wading bird use of estuarine islands in the Pacific Northwest, Technical Report D-78-17. Final Report by John Graham Company, Seattle, WA. 220 pp.
- Potts, G.R., J.C. Coulson, and I.R. Deans. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *Journal of Animal Ecology* 49:465-484.
- Raffaelli, D., H. Richner, R. Summers, and S. Northcott. 1990. Tidal migrations in the flounder (*Platichthys flesus*). *Marine Behavioural Physiology* 16:249-260.
- Ramsey, F.L., and D.W. Schafer. 1997. *The statistical sleuth: A course in methods of data analysis*. Wadsworth Publ. Co., Belmont, CA. 742 pp.
- Regehr, H.M., M.S. Rodway, and W.A. Montevecchi. 1998. Antipredator benefits of nest-site selection in Black-legged Kittiwakes. *Canadian Journal of Zoology* 76:910-915.
- Reise, K. 1985. *Tidal flat ecology: An experimental approach to species interactions*. Springer-Verlag, Berlin. 191 pp.
- Richner, H. 1995. Wintering cormorants *Phalacrocorax carbo carbo* in the Ythan estuary, Scotland: Numerical and behavioural responses to fluctuating prey availability. *Ardea* 83:193-197.
- Ricklefs, R.E. 1979. *Ecology*, 2nd ed. Chiron Press, Inc., New York, NY. 966 pp.

- Roby, D. D., D. P. Craig, K. Collis, and S. L. Adamany. 1998. Avian predation on juvenile salmonids in the lower Columbia River. 1997 Annual Report of the Oregon Cooperative Fish and Wildlife Research Unit at Oregon State University to Bonneville Power Administration and U.S. Army Corps of Engineers, Portland, OR. 148 pp.
- Rodway, M.S. 1991. Status and conservation of breeding seabirds in British Columbia. Pages 43-102 in J.P. Croxall (ed.), Seabird status and conservation: A supplement. Technical Publication No. 11. International Council for Bird Preservation, Cambridge, UK.
- Rolland, C. E., E. Danchin, and M. de Fraipont. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: A comparative analysis. *American Naturalist* 151:514-529.
- Rowe, S., and I.L. Jones. 2000. The enigma of Razorbill *Alca torda* breeding site selection: Adaptation to a variable environment? *Ibis* 142:324-327.
- SAS Institute Inc. 1999. SAS/STAT Software, Version 8. SAS Institute Inc., Cary, NC.
- Sauer, J.R., J.E. Hines, G. Gough, I. Thomas, and B.G. Peterjohn. 1997. The North American breeding bird survey results and analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, MD. At <http://www.mbr-pwrc.usgs.gov/bbs/>.
- Schjorring, S., J. Gregersen, and T. Bregnballe. 1999. Prospecting enhances breeding success of first-time breeders in the Great Cormorant, *Phalacrocorax carbo sinensis*. *Animal Behaviour* 57:647-654.
- Schreiber, R.W., and R.B. Clapp. 1987. Pelecaniform feeding ecology. Pages 173-188 in *Seabirds: Feeding ecology and role in marine ecosystems*. Cambridge University Press, New York, NY. 408 pp.
- Selander, R. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- Shugart, G.W., M.A. Fitch, and V.M. Shugart. 1981. Minimizing investigator disturbance in observational studies of colonial waterbirds: Access to blinds through tunnels. *Wilson Bulletin* 93:565-569.

- Siegel-Causey, D., and G.L. Hunt. 1981. Colonial defense behavior in Double-crested and Pelagic cormorants. *Auk* 98:522-531.
- Siegel-Causey, D., and G.L. Hunt. 1986. Breeding-site selection and colony formation in Double-crested and Pelagic cormorants. *Auk* 103:230-234.
- Siegel-Causey, D., and S.P. Kharitonov. 1990. The evolution of coloniality. Pages 285-330 in D.M. Power (ed.), *Current ornithology*. Vol. 7. Plenum, New York, NY.
- Simenstad, C.A., L.F. Small, C.D. McIntire, D.A. Jay, and C. Sherwood. 1990. Columbia River estuary studies: An introduction to the estuary, a brief history, and prior studies. *Progress in Oceanography* 25:1-13.
- Spear, L.B. 1993. Dynamic and effect of Western Gulls feeding in a subcolony of guillemots and Brandt's Cormorants. *Journal of Animal Ecology* 62:399-414.
- S-PLUS. 1999. S-plus 2000, Release 3. MathSoft, Inc., Seattle, WA.
- Suryan, R.M., D.B. Irons, M. Kaufman, J. Benson, P.G.R. Jodice, D.D. Roby, and E.D. Brown. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series* 236:273-287.
- Todd, C.S., L.S. Young, R.B. Owen, and F.J. Gramlich. 1982. Food habits of Bald Eagles in Maine. *Journal of Wildlife Management* 46:636-645.
- Trapp, J.L., S.J. Lewis, and D.M. Pence. 1997. Double-crested Cormorant impacts on sport fish: Literature review, agency survey, and strategies. Pages 17-26 in M.E. Tobin (ed.), *Symposium on Double-crested Cormorants: Population status and management issues in the Mid-west*. USDA/APHIS Tech. Bull. No. 1879. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Washington, DC. 164 pp.
- Trinast, E.M. 1975. Tidal currents and *Acaria* distributions in Newport Bay, California. *Estuarine and Coastal Marine Science* 3:165-176.

- Tyson, L.A., J.L. Belant, F.J. Cuthbert, and D.V. Weseloh. 1999. Nesting populations of Double-crested Cormorants in the United States and Canada. Pages 17-26 *in* M.E. Tobin (ed.), Symposium on Double-crested Cormorants: Population status and management issues in the Mid-west. USDA/APHIS Tech. Bull. No. 1879. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Washington, DC. 164 pp.
- USFWS (United States Fish and Wildlife Service). 1988. Endangered species act of 1973. As amended through the 100th Congress. U.S. Department of the Interior, Washington, D.C.
- USFWS (United States Fish and Wildlife Service). 2001. Draft environmental impact statement: Double-crested Cormorant management. United States Department of the Interior, Fish and Wildlife Service, Washington, DC. 152 pp.
- USNO (United States Naval Observatory). 2002. Sunrise/sunset and civil twilight tables for Astoria, Oregon in 2001. Astronomical Applications Department, Washington, DC. At <http://aa.usno.navy.mil/data/docs>.
- Van der Veen, H.E. 1973. Some aspects of the breeding biology and demography of the Double-crested Cormorants (*Phalacrocorax auritus*) of Mandarte Island. Ph.D. thesis, Zoologisch Laboratorium der Rijksuniversiteit te Groningen, Groningen *in* Hatch and Weseloh (1999).
- Van Eerden, M.R., and J. Gregersen. 1995. Long-term changes in the northwestern European population of cormorants. *Ardea* 83:61-79.
- Van Eerden, M.R., and B. Voslamber. 1995. Mass fishing by Cormorants *Phalacrocorax carbo sinensis* at Lake Ijsselmeer, the Netherlands: A recent and successful adaptation to a turbid environment. *Ardea* 83:199-212.
- van Tets, G.F. 1959. A comparative study of some social communication patterns in the Pelecaniformes. Ornithological Monograph No. 2: American Ornithologists' Union, Washington, DC.
- Verbeek, N.A.M. 1982. Egg predation by Northwestern Crows: Its association with human and Bald Eagle activity. *Auk* 99:347-352.

- Voslamber, B., M. Platteeu, and M.R. Van Eerden. 1995. Solitary foraging in sand pits by breeding cormorants *Phalacrocorax carbo sinensis*: Does specialized knowledge about fishing sites and fish behaviour pay off? *Ardea* 83:213-222.
- Wanless, S., M.P. Harris, and J.A. Morris. 1995. Factors affecting daily activity budgets of South Georgian Shags during chick rearing at Bird Island, South Georgia. *Condor* 97:550-558.
- Watanuki, Y., A. Kato, and Y. Naito. 1996. Diving performance of male and female Japanese Cormorants. *Canadian Journal of Zoology* 74:1098-1109.
- Watson, J.W., M.G. Garrett, R.G. Anthony. 1991. Foraging ecology of Bald Eagles in the Columbia River estuary. *Journal of Wildlife Management* 55:492-499.
- Weimerskirch, H., O. Chastel, L. Ackermann, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeier, and J. Judas. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* 47:472-476.
- Weseloh, D.V.C., and P.J. Ewins. 1994. Characteristics of a rapidly increasing colony of Double-crested Cormorants (*Phalacrocorax auritus*) in Lake Ontario: Population size, reproductive parameters and band recoveries. *Journal of Great Lakes Research* 20:443-456.
- White, G.C., and R.A. Garrott. 1990. *Analysis of Wildlife Radio-tracking Data*. Academic Press, Inc., New York, NY. 383 pp.
- Whitfield, A.K., and S.J.M. Blaber. 1979. Feeding ecology of piscivorous birds at Lake St. Lucia. Part 3. Swimming Birds. *Ostrich* 50:10-20.
- Wilson, U.W. 1991. Responses of three seabird species to El Niño events and other warm episodes on the Washington coast, 1979-1990. *Condor* 93:853-858.
- Wires, L.R., F.J. Cuthbert, D.R. Trexel, and A.R. Joshi. 2001. Status of the Double-crested Cormorant (*Phalacrocorax auritus*) in North America. Final Report to United States Fish and Wildlife Service. University of Minnesota, St. Paul, MN. 360 pp.
- Wirjoatmodjo, S., and T.J. Pitcher. 1984. Flounders follow the tides to feed: Evidence from ultrasonic tracking in an estuary. *Estuarine, Coastal and Shelf Science* 19:231-241.

- Wittenberger, J.F., and G.L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. Pages 1-78 *in* D.S. Farner, J.R. King, and K.C. Parkes (eds.), *Avian biology*. Vol. 8. Academic Press, Inc., New York, NY. 256 pp.
- Wolff, W.J., M.A. Mardos, and A.J.J. Sandee. 1981. Tidal migration of plaice and flounders as a feeding strategy. Pages 159-171 *in* Jones, N.J., Wolff, W.J. (eds.), *Feeding and survival strategies of estuarine organisms*. Plenum Press, New York, NY. 304 pp.
- Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443-466.
- Wright, H.W. 1913. The birds of San Martín Island, Lower California. *Condor* 15:207-210.
- Zamon, J.E. 2000. The influence of tidal currents on plankton densities and energy flow to seals, seabirds, and schooling fishes in the San Juan Islands, Washington, USA. Ph.D. thesis, University of California, Irvine, CA. 181 pp.
- Zar, J.H. 1984. *Biostatistical analysis*, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 pp.