

Keynote Address

The Problems of Being Successful: Managing Interactions Between Humans and Double-Crested Cormorants

By Douglas Siegel-Causey

Abstract: The natural history, behavior, and ecology of double-crested cormorants (Phalacrocorax auritus) predispose this species for conflict with human sport and commercial fisheries. Cormorants breed early in life, have large broods, are efficient predators even in marginal conditions, seem to be able to adjust colony sizes quickly in response to local conditions, and have limited requirements for feeding and nesting habitats. A survey of the past history of successes and failures in managing cormorants reveals that

This paper is meant to provide a brief look into the our world with the diversity of birds, and most would natural history, behavior, and conservation ecology of without them.

an increasingly common water bird of continental North America and to examine how these aspects place it in conflict with human activities. I will partially survey the history of successes and failures in how humans have dealt with double-crested cormorants (DCCO's) as a problem species and review some of the developments in approaches undertaken in the past 5 years since the 1992 symposium on this topic held in Oxford, MS, that was sponsored by the Colonial Waterbird Society (Nettleship and Duffy 1995). Finally, I will provide some insights that may help alleviate the impact of current and future problematic consequences of human activities on the natural activities of the DCCO.

From the beginning, the scientific and popular literature on cormorants has been dominated by practical and domestic topics of management and pest control, which relate ultimately to the ubiquity of these birds, their natural history and ecology, and their proximity to human activities. Of the roughly 10,000 species of birds, only a few have achieved the status of pests. Depending upon the gaze of the beholder, most are seen as being critical components of local ecosystems, as unique subjects for scientific investigation, or as pleasant components of the natural world. Even those of us with little interest in environmental issues or wildlife ecology seem to appreciate sharing

economic impact is greatest with aquaculture and least in sport fisheries. Research during the past 5 years suggests that some control methods like culling and egg spraying are effective but must be balanced against the actual impacts on humans.

Keywords: aquaculture, conflict, diet, double-crested cormorant, feeding ecology, fisheries, natural history, pests, Phalacrocoracidae, Phalacrocorax auritus, management

agree that this would be a drab and dismal world

Those birds achieving the rare status of a problem species have, therefore, done so by factors that are entirely extrinsic and anthropocentric. That is, a pest is acknowledged as such by human perceptions based on many personal assessments of sociological and economic value, desirability, and even beauty. I think that most people would agree that neither these nor other such criteria are the result of evolutionary selection or ecological process but instead are a consequence of human activities, culture, and behavior. Where human perceptions and natural history clash, the conflicts usually result in severe impacts on individuals and populations of the pest species sometimes to its ultimate detriment.

There is a fairly extensive literature associated with the issues of pest or problem species (see Kellert 1985 and Wagner and Seal 1992 for helpful reviews), and there have been several recent symposia dealing specifically with human-cormorant conflicts (Nettleship and Duffy 1995, van Eerden et al. 1995). This paper will serve instead as a survey of those aspects of DCCO biology that create conditions for pestiferous status and as an introduction for the following papers which focus on developments, positive and negative, that have occurred in the past 5 years.

Cormorant Systematics and Evolutionary Relationships

Cormorants and shags (Phalacrocoracidae) are the most successful family of the Order Pelecaniformes and comprise at least 35 species worldwide. Birds of this family are generally found near coastal and nearshore waters, and they are common dwellers in marine and freshwater littoral habitats. They are restricted from oceanic habitats chiefly because of their unique wettable plumage, a feature well suited for underwater pursuit of shallow-bottom-dwelling fish but one that requires perching sites for drying and thermoregulation. Consequently, members of this group are found along most of the productive coastlines world-

wide (except in polar regions), and often far inland following major freshwater drainages.

The Family Phalacrocoracidae has long been considered to be a homogeneous group. Recent systematic study revealed instead that there are two well-defined groups in the family: cormorants and shags (Siegel–Causey 1988). Shags characteristically are compact, offshore foragers that are flat- and cliffnesting birds with fair flight abilities. By contrast, cormorants can be generalized as heavy-bodied, deep-feeding near-shore foragers that prefer flat- and tree-nesting and have indifferent or labored flight.

There are four taxonomic groups within cormorants (fig. 1): the microcormorants ("Little"), the marine cormorants, the macrocormorants ("Great"), and the

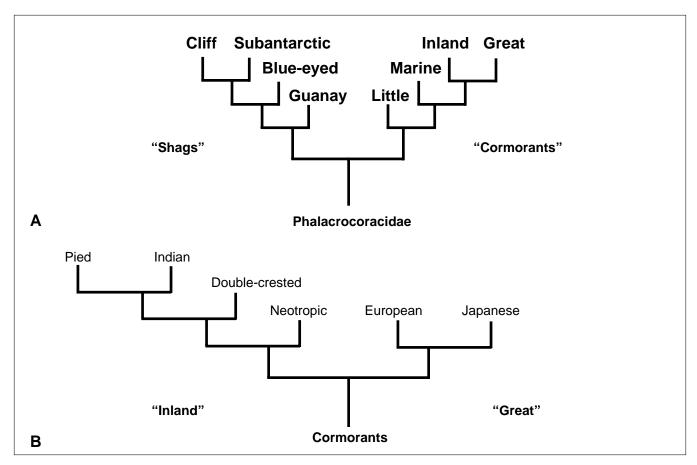


Figure 1—Phylogenetic relationships of cormorants. A = genera of shags and cormorants; B = species of inland and great cormorants. Latin names of cormorant species are pied cormorant (*Phalacrocorax*)

varius), indian cormorant (*P. sulcirostris*), double-crested cormorant (*P. auritus*), neotropic cormorant (*P. brasilianus*), European or great cormorant (*P. carbo*), and Japanese cormorant (*P. capillatus*).

mesocormorants ("Inland")(Siegel–Causey 1988). The latter group is composed of entirely black or dark birds having broad geographic distributions. With a few exceptions, these are the only members of the family to inhabit the continental interiors extensively. The mesocormorants include two of the most common cormorants of the New World: the olivaceous cormorant (*Phalacrocorax brasiliensis*) and the DCCO. These two species have complementary distributions

extending from Tierra del Fuego to Canada, from the Atlantic and Caribbean shores to the Pacific and, with the great cormorant (*P. carbo*), are undoubtedly the most studied members of the family (Lewis 1929, Mendall 1935, Palmer 1962, Hatch and Weseloh 1999).

The DCCO is commonly considered to comprise six allopatric breeding populations that serve as the basis for the current taxonomy of five subspecies (see

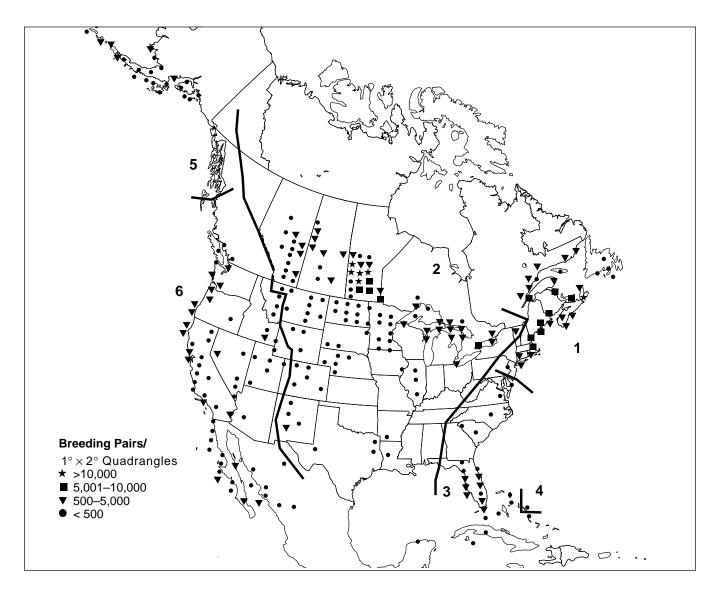


Figure 2—Populations of double-crested cormorants: 1 = Atlantic (northeast coast), 2 = Interior, 3 = Florida and Caribbean, 4 = San

Salvador, 5 = Alaska, and 6 = west coast. The symbols indicate numbers of breeding pairs in 1:250,000 quadrangles (1°N. by 2°W.).

Siegel-Causey and Litvinenko 1993, Hatch 1995, and Hatch and Weseloh 1999 for greater detail). P. a. auritus, the nominal race, is found throughout most of interior and northeast North America. P. a. albociliatus breeds extensively on the west coast of North America up to southern British Columbia. P. a. cincinatus is found from southern British Columbia up to Alaska. P. a. floridanus is found in the eastern gulf coast regions, eponymously in Florida. And P. a. heuretus, resides on San Salvador Island and other islands of the Caribbean (fig. 2). Most of the populations are migratory—P. a. floridanus and P. a. heuretus appear to be sedentary, however-but patterns of nonbreeding movement are not well known, and there appears to be some intermixing between adjacent populations (Hatch 1995, Hatch and Weseloh 1999). The interior and Atlantic breeding populations are migratory in the sense that there is substantial postbreeding dispersal away from the breeding colonies. In some localities, seasonal longrange dispersal may be specific by demography, gender, or reproductive success (Palmer 1962, Godfrey 1986, Johnsgard 1993, Chapdelaine and Bédard 1995, Krohn et al. 1995, Thompson et al. 1995, Weseloh et al. 1995, Hatch and Weseloh 1999). The source of much of the current controversy surrounding cormorant depredations lies in the increasing size and expanding migratory movements of the interior population (Price and Nickum 1995).

The interior population is strongly migratory and has its population center in the northern prairies and Great Lakes States (fig. 2). The population is robust and is increasing rapidly, although until the 1980's it was in decline (Vermeer and Rankin 1984, Root 1988, Hobson et al. 1989, Dolbeer 1991, Weseloh and Collier 1995). The largest concentrations of wintering birds tend to be along the gulf coast of Mexico and the Southern United States, and the flood plain of the lower Mississippi (Root 1988, Dolbeer 1991, Nettleship and Duffy 1995, Weseloh and Collier 1995). It is these wintering populations and their explosive increase in the past decade that are the source of much of the trouble experienced with DCCO's and human aquaculture activities. How cormorant biology sets up this species for conflict is the subject of the next section.

Natural History and Behavior of DCCO's

Nests and pestilence are terms essentially relating to human interactions, although there is some biological justification for using these terms to characterize DCCO's. Several features can distinguish biological pests, including the following nonobjective anthropocentric criteria: overabundant populations, rapid population growth, noisome behavior, impacts on human health and safety, and costs for control, mitigation, and cleanup. Duffy (1995) has detailed many of these relative to DCCO—human interactions.

Nesting Requirements

Cormorants have very flexible requirements for nesting and nest construction and are known to breed in several habitat types, including on level ground, on cliffs and embankments, in trees, on bridge supports, on wharf piles—in short, on most objects large and stable enough to support the weight of the nest and contents while affording some protection from ground predators, such as mammals and reptiles (Siegel-Causey and Hunt 1981, Siegel-Causey 1988). Proximity to water is an absolute requirement because cormorants are nearly exclusively piscivorous, and the size of breeding colonies in continental interiors correlates with how close they are to feeding areas (fig. 3). Freshwater and marine islands, shoreline and bank vegetation, isolated stands of trees near water, and bluffs serve as suitable nesting sites. All are found throughout the range of the interior population, but the greatest concatenation of these habitat parameters occurs around the Great Lakes (Hatch and Weseloh 1999). Not surprisingly, the greatest breeding populations of DCCO's are found around the Great Lakes, although nearly every State and Province has scattered breeding colonies (Hatch 1995).

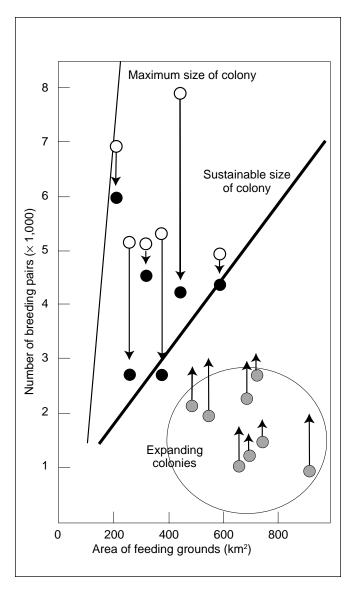


Figure 3—Colony size (breeding pairs) in relation to available feeding habitat (0–20 m water depth) without overlap with other colonies with a range of 20 km from the colony. Maximum colony size (open circles) and, if different, most recent colony size (dark circles) indicate effects of oversaturation of feeding resources. The recent colonies in Denmark (shaded circles) are undersaturated with respect to available feeding resources and are fast expanding in size. Both effects suggest the existence of a "sustainable" and a "maximum" density. The oversaturation effect is particularly noticable in the Brændegård colony (1) in Denmark. Numbers refer to monitored colonies: 1–3 = Denmark, 4–6 = The Netherlands, 1 = Brændegård, 2 = Vorsø, 3 = Bognæs, 4 = Naardermeer, 5 = Lepelaar plassen, 6 = Oostvaarders plassen. Redrawn with permission from van Eerden and Gregersen (1995).

In summary, DCCO's are well suited for the Midwest because the habitats required for nesting and feeding young are those that are commonly found throughout the Midwest. Consequently, cormorants are found throughout the interior of North America, and their numbers are limited in the sense of the size of the colony rather than in their distribution. The exception is that cormorants are rarely seen in the prairies, that is, west of the Missouri River, where they are excluded by having limited access to water and trees.

Morphology

By their morphology, cormorants are very efficient and guick in swimming. All four toes are webbed together, the hindlimbs are set far back on the body, the outer part of the plumage accepts water and thus affords negative buoyancy, and birds are darkly camouflaged (Nelson 1980, Siegel-Causey 1988). The serrated edges of the bill and the terminal hook help them to grasp fish securely, the small xiphoid bone at the back of the head and nasal-frontal hinge between the skull and bill allow the mouth to be opened widely while underwater, and the proventriculus region above the stomach is expandable which allows a substantial amount of fish to be swallowed in one feeding bout (Owre 1967, Ainley 1977, Ainley et al. 1981). What further aids them in fish capture is that their eyes are able to accommodate about 30 diopters and apparently are quite sensitive to movement (Sivak et al. 1977). These and other adaptations enable cormorants to pursue and capture small fish very efficiently in clear-water streams and lakes; in addition, several other features of behavior and ecology may play a role in less optimal habitats.

Feeding Behavior

Johnsgard (1993) and Duffy (1995) summarize the literature on foraging ecology quite well. DCCO's are almost exclusively piscivorous and pursue prey underwater. By virtue of wing morphology and aerodynamics, cormorants are indifferent fliers and do not range far from roosting or breeding areas (Ainley 1977, Pennycuick 1989 and 1991). Colony and perch sites as a consequence are located near foraging areas,

tend to be patchily distributed throughout the landscape, and concentrate large numbers of birds (Kharitonov and Siegel–Causey 1988). There is ongoing debate whether birds in colonies share information in some way about feeding areas (Siegel– Causey and Kharitonov 1990), but the phenomenon of social feeding in cormorants is well observed (e.g., Bartholomew 1942, Van Eerden and Voslamber 1995).

Social or mass feeding takes place when dense flocks of birds aggregate to concentrate prey by walking, herding, diving, or in the case of cormorants, pursuing. In the most detailed studies to date, Van Eerden and Voslamber (1995) were able to document a change in feeding behavior over 2 decades by great cormorants breeding on Lake Ijsselmeer in Holland, from entirely solitary fishing to mass feeding. Two patterns were identified: line hunting, in which birds move through the water in a straight line in a rolling flock, and zigzag hunting, in which individuals search and change directions. Line hunting was associated with smaller fish like smelt (Osmerus eperlanus) and ruffe (Gymnocephalus cernuus), whereas zigzag fishing was recorded when cormorants were catching larger fish (> 15 cm) like roach (Rutilus rutilus) and perch (Perca fluviatilis). Mean swimming speeds were greater during zigzag hunting compared to line-hunting (1.33 v. 1.04 ms⁻¹). These behaviors are very effective for hunting fish in turbid waters, and the changes from solitary to mass feeding are associated with the increasing turbidity of the foraging areas used by cormorants. On the basis of echo soundings, observations of cormorants underwater, and capture rates, the effect of different light levels on diet underwater has been related to the vertical distribution of fish. During daytime, most fish tend to stay at depths below 1 percent of the light at the surface. At intermediate light levels in the water, cormorants drive the fish from the dark zone into the clear top layer, where they are caught by social flocks of swimming birds. Thus, Van Eerden and Voslamber (1995) concluded that deteriorating visibility, increased cormorant populations, and increased abundance of small fish all were factors contributing to a behavioral switch in feeding.

Population Dynamics

Cormorants have a relatively early onset of breeding (Palmer 1962, van de Veen 1973). They sometimes begin breeding during the first or second year. They have relatively large clutches compared with other seabirds (Duffy 1980, Siegel-Causey 1988) and are able to relay even entire clutches (Palmer 1962, Hatch and Weseloh 1999). Egg laying and hatching are asynchronous, likely related to food supply (Williams and Burger 1979), and seem to allow for a quick response to environmental conditions. Reproductive success can vary substantially, but values of 1.5 to 3.5 young per nest are typically recorded (Drent et al. 1964, Price and Weseloh 1986). That value is high for seabirds (Lack 1967, Johnsgard 1993). Prebreeding mortality rates of 50 to 70 percent are typical for large water birds, but where subadult survival is enhanced through abundant food supply over the first year, mortality rates drop to 35 percent or less (Price and Weseloh 1986).

Population levels of DCCO's have changed dramatically in the Great Lakes region, showing a gradual decline over 2 decades up until the mid-1960's and then a rapid and dramatic increase starting in the early 1980's (Price and Weseloh 1986, Weseloh et al. 1995). The causes for the decline are still unclear, but contaminant-related egg-shell thinning and human disturbance are strongly implicated (Weseloh and Collier 1995). The causes for the dramatic increase are related directly to high DCCO productivity and survival rates: in the Great Lakes populations, the annual rate of increase was about 35 percent, which translates into a doubling of population every 3 years (Weseloh and Collier 1995). The ecological factors that helped fuel this increase are the subject of continuing study, but it is clear nonetheless that cormorant populations can increase rapidly, given suitable conditions.

There is evidence from European studies on great cormorants suggesting that the size of individual colonies tracks the ecological availability of resources utilized by colony members (fig. 3). In studies conducted in the last decade on the population

dynamics of Dutch and Danish cormorant colonies, van Eerden and Gregersen (1995) found that old colonies experienced population reductions in association with reduction in nearby feeding areas. By contrast, newly established colonies experienced rapid growth in colony size, and the rate of expansion was related as well to the size of the feeding area. Van Eerden and Gregersen concluded that the number of breeding pairs found in colonies was related to the sustainable size of colonies, which was optimally related to the area of shallow water (i.e., less than 20 m) suitable for feeding. In other words, it appeared that great cormorants were regulating colony sizes by means yet not understood, using some yet unknown assessment of available resources that is apparently independent of the availability of nesting habitat. If true, this means that cormorants can fine-tune local numbers in response to changing conditions nearby.

The Past 5 Years

The papers that follow in the symposium detail some of the advances made in understanding the nature of human-cormorant interactions in North America since the pioneering symposia of Nettleship and Duffy (1995) and van Eerden et al. (1995), particularly those involving DCCO's in the Great Lakes region of the United States and Canada and aquaculture operations in the delta region of Mississippi. Increases in breeding populations have not been uniform over the range of this species, and stable or slight decreases have been seen in the western populations (0 to -7 percent), moderate increase in southern populations (+3 percent), and great increase in interior (+8 percent) and Great Lakes (+18 percent) populations (Tyson et al., this volume). Ongoing study of the possible causes for these dynamics has indicated consistent with the results of previous work published elsewhere, that population increases are likely due to reduced control measures in breeding areas, reduced contaminant loads, and increased reproductive success probably

reflecting human-related availability of forage fish in aquaculture ponds. Population decreases are likely related to large-scale environmental effects, such as destruction or reduced availability of breeding habitat and feeding areas.

Quantitative and fine-scale study of the diet of DCCO's feeding in areas heavily used for human activities in the Great Lakes revealed that seasonal impacts were likely to be great, but the annualized effect was generally minimal on economically important fish species. For example, Belyea et al. (this volume) found that, although nearly half of the spring diet of DCCO's feeding in northern Lake Huron was yellow perch, economically unimportant fish such as alewife and sticklebacks were far more important on a yearly budget. By contrast, Bur et al. (this volume) found greater diversity in cormorant diet (yellow perch, shiners, gizzard shad, alewife, and trout perch) collected on western Lake Erie. They concluded that the diets varied seasonally and did not indicate that cormorants were serious predators or competitors of commercially valuable fish.

Bédard and colleagues (this volume) followed up their study first presented in 1995 (Bédard et al. 1995) with results showing that egg spraying and culling reduced the breeding population in the St. Lawrence River estuary from about 17,000 to 10,000 pairs in only 4 years. These measures were quite effective at reducing numbers, but the authors were not convinced that they were practical given the investment needed in effort and resources balanced against the minimal economic impact of the cormorants on sport fisheries. A review of published studies and a survey of agency management successes (Trapp et al., this volume) showed that, although the economic impact of cormorants on sport fisheries was minimal and biologically unwarranted, the impact was high and localized in regions with high aquaculture use. On the basis of these and other factors, the U.S. Fish and Wildlife Service allows control measures, including removal by shooting, of DCCO's feeding on catfish farms in the Mississippi Delta.

The Predatory Cormorant

The natural history, ecology, and adaptability of DCCO's to changing conditions are all factors that characterize this species as a particularly responsive and effective fish predator. This is a fact not unnoticed by aquaculturists, the sport fisheries community, and natural resource managers, all of whom have outlooks that differ from those concerned with preserving natural environments and ecosystem function. In a review of earlier symposia (Nettleship and Duffy 1995, van Eerden et al. 1995) devoted to the issue of DCCO human interactions, Nisbet (1995) characterized this conflict succinctly:

The scientists tended to concentrate on gaps in knowledge of the species and the need for further research, and were often critical of what they perceived as lack of rigor in the work done on depredation and management techniques. The aquaculturists tended to concentrate on mechanisms of control and were impatient with what they perceived as pedantry in demands for more detailed investigation of the obvious. Representatives of wildlife management agencies were situated uncomfortably in between these two groups, recognizing both the need for better knowledge and the pressure for prompt action.

Cormorant–human conflict has existed no doubt as long as both have shared the same resources. As discussed here and elsewhere, the natural history and ecology of DCCO's, the introduction of an abundant and widespread feeding resource—catfish aquaculture ponds—adjacent to their wintering range, and lessening of pollution effects in the breeding range have all played a role in the rapid expansion in abundance and distribution of DCCO's. What distinguishes the present situation from similar circumstances in the past is the scale of the problem. That is, the number of birds is larger, the economic value at risk is greater, and the numbers of people and their enterprises are greater. The essential nature of the conflict, however, remains the same.

Careful reading of the general conclusions of the studies discussed here and others related to conflict between human activities and cormorant activities reveals to me the following common realities:

- 1. There is a direct relation between the perception of cormorants as pests and their ubiquity. The natural history and ecology of DCCO's are features that predate our arrival, and it is humans, not cormorants, who have altered the environmental conditions. A generation ago, cormorants were rare but not unknown in regions such as the Mississippi Delta and, although depredations on aquaculture operations occurred, they were as sporadic and widespread as the ponds themselves. With increased numbers of humans and cormorants comes increased interactions and increased conflict. In cases such as the Midwestern United States and Great Lakes region, sociological factors may play nearly as large a role as do the actual economics of loss (Wagner and Seal 1992, Duffy 1995). In others, as with catfish aquaculture in the Southern United States, economic impacts of cormorant depredation are substantial.
- 2. Although local control of cormorants can often control local situations, the effort has minimal effect on regional problems because the size and geographic extent of DCCO populations are several orders of magnitude greater. In other words, despite whether extirpation is possible on local scales, a massive effort would be required in both wintering and breeding areas to accomplish an effective reduction in numbers.
- 3. Human activities, not those of cormorants, are the novel perturbation in this natural system. Putting esthetics aside, this means that the most effective resolution of human-cormorant conflicts will be in those contexts where the consequences of human activities (construction of point-source, high-density food resources like aquaculture ponds, proliferation of roosting and breeding habitat like marginal and emergent vegetation, etc.) are managed rather than those of the birds themselves.

References Cited

- **Ainley, D. G. 1977**. Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In: Llano, G., ed. Adaptations within antarctic ecosystems. Washington, DC: Smithsonian Institution Press: 669–685.
- Ainley, D. G.; Anderson, D. W.; Kelly, P. R. 1981. Feeding ecology of marine cormorants in southwestern North America. Condor 83: 120–131.
- **Bartholomew, G. A., Jr. 1942.** The fishing activities of double- crested cormorants in San Francisco Bay. Condor 44: 13–21.
- **Bédard, A.; Nadeau, A.; Lepage, M. 1995.** Double-crested cormorant culling in the St. Lawrence River estuary. Colonial Waterbirds 18 (Spec. Publ. 1): 78–85.
- Chapdelaine, G.; Bédard, J. 1995. Recent changes in the abundance and distribution of the double-crested cormorant in the St. Lawrence River, estuary, and gulf, Quebec. Colonial Waterbirds 18 (Spec. Publ. 1): 70–77.
- **Dolbeer, R. A. 1991.** Migration patterns of double-crested cormorants east of the Rocky Mountains. Journal of Field Ornithology 62: 83–93.
- **Drent, R.; van Tets, G. F.; Tompa, F.; Vermeer, K. 1964.** The breeding birds of Mandarte Island, British Columbia. Canadian Field-Naturalist 78: 208–263.
- **Duffy, D. C. 1980.** Comparative reproductive behavior and population regulation of seabirds of the Peruvian coastal current. Ph.D. dissertation. Princeton, NJ: Princeton University Press.
- **Duffy, D. C. 1995.** Why is the double-crested cormorant a problem? Insights from cormorant ecology and human sociology. Colonial Waterbirds 18 (Spec. Publ. 1): 25–32.
- **Godfrey, W. E. 1986.** The birds of Canada, rev. ed. Ottawa, ON: National Museum of Natural Sciences, National Museums of Canada.
- **Hatch, J. J. 1995.** Changing populations of double-crested cormorants. Colonial Waterbirds 18 (Spec. Publ. 1): 8–24.

- Hatch, J. J.; Weseloh. D. V. 1999. The double-crested cormorant. In: Poole, A.; Gill, F., eds. The Birds of North America. No. 441. Philadelphia: The Birds of North America, Inc.
- Hobson, K. A.; Knapton, R. W.; Lysack, W. 1989. Population, diet, and reproductive success of double-crested cormorants breeding on Lake Winnipegosis, Manitoba in 1987. Colonial Waterbirds 12: 191–197.
- **Johnsgard, P. A. 1993.** Cormorants, darters, and pelicans of the world. Washington, DC: Smithsonian Institution Press.
- **Kellert, S. R. 1985.** Historical trends in perception and uses of animals in twentieth-century America. Environmental Review 9: 19–33.
- **Kharitonov, S. P.; Siegel–Causey, D. 1988.** Colony formation in seabirds. Current Ornithology 5: 223–272.
- Krohn, W. B.; Allen, R. B.; Moring, J. R.; Hutchinson, A. E. 1995. Double-crested cormorants in New England: population and management histories. Colonial Waterbirds 18 (Spec. Publ. 1): 99–109.
- **Lack, D. 1967.** Interrelationships in breeding adaptations as shown by marine birds. Proceedings of the International Ornithological Congress 14: 3–31.
- **Lewis, H. F. 1929.** The natural history of the double-crested cormorant *(Phalacrocorax auritus auritus [Lesson])*. Ottawa, ON: Ru-Mi-Lou Books.
- **Mendall, H. L. 1935.** The home-life and economic status of the double-crested cormorant *Phalacrocorax auritus auritus* (Lesson). Maine Bulletin 39: 1–159.
- **Nelson, J. B. 1980.** Seabirds, their biology and ecology. New York: Hamlyn.
- **Nettleship, D. N.; Duffy, D. C., eds. 1995.** The double-crested cormorant: biology, conservation, and management. Colonial Waterbirds 18 (Spec. Publ. 1): 1–256.
- **Nisbet, I.C.T. 1995.** Concluding remarks. Colonial Waterbirds 18 (Spec. Publ. 1): 242–249.
- **Owre, O. T. 1967.** Adaptations for locomotion and feeding in the anhinga and double-crested cormorant. Ornithological Monograph 6: 1–138.

- **Palmer, R. S., ed. 1962.** Handbook of North American birds, vol. 1. New Haven, CT: Yale University Press.
- **Pennycuick, C. J. 1989.** Span-ratio analysis used to estimate effective lift:drag ratio in the double-crested cormorant *Phalacrocorax auritus* from field observations. Journal of Experimental Biology 142: 1–15.
- **Pennycuick, C. J. 1991.** Flight of seabirds. In: Croxall, J. P., ed. Seabirds: feeding ecology and role in marine ecosystems. Cambidge, UK: Cambridge University Press: 43–62.
- **Price, I. A.; Weseloh, D. V. 1986.** Increased numbers and productivity of double-crested cormorants *Phalacrocorax auritus* on Lake Ontario. Canadian Field-Naturalist 100: 474–482.
- **Price, I. M.; Nickum, J. G. 1995.** Aquaculture and birds: the context for controversy. Colonial Waterbirds 18 (Spec. Publ. 1): 33–45.
- **Root, T. L. 1988.** Atlas of wintering North American birds. Chicago: University of Chicago Press.
- **Siegel–Causey, D. 1988.** Phylogeny of the Phalacrocoracidae. Condor 90: 885–905.
- **Siegel–Causey, D.; Hunt, G. L., Jr. 1981.** Colonial defense behavior in double-crested and pelagic cormorants. Auk 98: 522–531.
- **Siegel–Causey, D.; Kharitonov, S. P. 1990.** The evolution of coloniality. Current Ornithology 7: 285–330.
- Siegel–Causey, D.; Litvinenko, N. M. 1993. Status, ecology, and conservation of shags and cormorants of the temperate North Pacific. In: Vermeer, K.; Briggs, K. T.; Morgan, K. H.; Siegel–Causey, D., eds. The status, ecology, and conservation of marine birds of the North Pacific. Spec. Publ. Ottawa, ON: Canadian Wildlife Service: 122–130.
- **Sivak, J. G.; Lincer, J. L.; Bobier, W. 1977.** Amphibious visual optics of the eyes of the double-crested cormorant *(Phalacrocorax auritus)* and the brown pelican *(Pelecanus occidentalis)*. Canadian Journal of Zoology 55: 782–788.
- Thompson, B. C.; Campo, J. J.; Telfair, R. C. 1995. Origin, population attributes, and management conflict resolution for double-crested cormorants wintering in Texas. Colonial Waterbirds 18 (Spec. Publ. 1): 181–188.

- van de Veen, H. E. 1973. Breeding biology and demography of the double-crested cormorant *Phalacrocorax auritus*. M.S. thesis. The Netherlands: University of Groningen.
- van Eerden, M. R.; Gregersen, J. 1995. Long-term changes in the northwest European population of cormorants *Phalacrocorax carbo sinensis*. Ardea 83: 61–80.
- van Eerden, M. R.; Voslamber, B. 1995. Mass fishing by cormorants *Phalacrocorax carbo sinensis* at Lake ljsselmeer, The Netherlands: a recent and successful adaptation to a turbid environment. Ardea 83: 199–212.
- van Eerden, M. R.; Koffijberg, K.; Platteeuw, M.; Zijlstra, M., eds. 1995. Proceedings of 1989 workshop on cormorants (*Phalacrocorax carbo*). Ardea 83: 1–338.
- **Vermeer, K.; Rankin, L. 1984.** Population trends in nesting double-crested and pelagic cormorants in Canada. Murrelet 65: 1–9.
- Wagner, F. H.; Seal, U. S. 1992. Values, problems, and methodologies in managing overabundant wildlife populations: an overview. In: McCullough, D. R.; Barrett, R. H., eds. Wildlife 2001: populations. London: Elsevier Scientific Publications: 279–293.
- Weseloh, D. V.; Collier, B. 1995. The rise of the double-crested cormorant on the Great Lakes: winning the war against contaminants. Great Lakes Fact Sheet EN 40–222/2–1995E. Ottawa, ON: Environment Canada.
- Weseloh, D. V.; Ewins, P. J.; Struger, J.; Mineau, P.; Bishop, C. A.; Postupalsky, S.; Ludwig, J. P. 1995. Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproductive output between 1913 and 1991. Colonial Waterbirds 18 (Spec. Publ. 1): 48–59.
- **Williams, A. J.; Burger, A. E. 1979.** Aspects of the breeding biology of the imperial cormorant *Phalacrocorax atriceps,* at Marion Island. Gerfaut 69: 407–423.