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Research Article

Aquaculture Depredation by Double-Crested Cormorants Breeding in Eastern North America

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ABSTRACT The double-crested cormorant (*Phalacrocorax auritus*) has undergone population expansion throughout much of its historical range since the 1970s, resulting in increased pressure on foraging habitats including real and perceived competition with commercial and sport fisheries and impacts on the aquaculture industry. The specific objectives of this study were to determine the stable isotope ratios of birds wintering at aquaculture facilities and natural freshwater and marine habitats, and to determine what percent of birds at distinct breeding colonies wintered in each of these habitats. We exploited natural variation in isotopic ratios of carbon, nitrogen, and sulfur (from feathers) to determine the winter habitat use (i.e., aquaculture, natural freshwater, or marine) of birds collected on their summer breeding grounds in the eastern United States (from Minnesota to Vermont). The distribution of winter habitat use varied significantly across breeding colonies and between male and female cormorants. More specifically, use of aquaculture winter habitat was most prevalent in birds breeding in Lake Huron and Lake Erie. Overall, aquaculture habitats were used more by males, and marine habitats were used more by females. The stable isotope approach used in this study provided dietary confirmation of previously observed migratory patterns in the double-crested cormorant. Because aquaculture was primarily used by males, and these males migrated to a broad range of breeding colonies, we suggest that targeting breeding birds to reduce aquaculture depredation is a less efficient strategy than managing birds at depredation sites on the wintering grounds. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS aquaculture, carbon-13, catfish, diet, double-crested cormorant, migration, nitrogen-15, *Phalacrocorax auritus*, sulfur-34.

Since the 1970s, the double-crested cormorant (*Phalacrocorax auritus*), a piscivorous colonial waterbird native to North America, has undergone rapid population expansion throughout much of its historical range (Hatch 1995, Hatch and Weseloh 1999, Weseloh et al. 2002, Ridgway et al. 2006, Wires and Cuthbert 2006). Population increases have been ascribed to lower mortality due to decreased contaminant levels, reduced human persecution, and increased food sources including aquaculture (Glahn et al. 1997, Hatch and Weseloh 1999, Glahn and King 2004). Resulting cormorant abundance may place increasing pressure on foraging and nesting habitats. Cormorants can reduce habitat quality and destroy vegetation when nesting at high densities (Hebert et al. 2005, Craig et al. 2012, Kolb et al. 2012) and may compete for

nesting habitat with co-occurring colonial waterbird species when nesting in mixed species colonies (Cuthbert et al. 2002; Weseloh et al. 2002; Somers et al. 2007, 2011). Cormorants have also been implicated in a range of human conflict issues including competition with commercial and sport fisheries (Taylor and Dorr 2003, Rudstam et al. 2004, Diana et al. 2006, Dorr et al. 2012b), and impacts to aquaculture facilities (Glahn et al. 2002, Glahn and King 2004, Dorr et al. 2012a). Cormorants wintering at catfish (*Ictalurus punctatus*) farms in the southeastern United States impose an annual burden of nearly \$25 million (U.S.) through predation on fish and associated management costs (Glahn et al. 2002). Pressure from the aquaculture industry, and from commercial and sport fishermen, has led to increased control efforts for cormorant populations at wintering and breeding grounds (Glahn et al. 2000a,b, 2002; Tobin et al. 2002; Diana et al. 2006).

Studies have examined cormorant diet and foraging behavior using a variety of methods including visual observations, satellite and radio tracking, bioenergetic

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modeling, and stomach content, regurgitant, and pellet analysis (Glahn and Brugger 1995, King et al. 1995, Neuman et al. 1997, Glahn and Dorr 2002, Rudstam et al. 2004). These methods identify components of diet consumed at the moment of observation but not the sum total of the animal's diet. In contrast, stable isotope ratios including carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) are based on the entire diet of an animal, and have therefore been recognized as highly valuable tools for assessing foraging ecology and migratory behavior in many species, including cormorants (Chang et al. 2008, Hebert et al. 2008, Hobson 2009, Doucette et al. 2011, Ofukany et al. 2012). In particular, stable isotope values from feathers reflect a bird's diet over the timescale of feather growth, and contain information about the relative importance of foraging resources during that period (Hobson and Clark 1992a,b; Hobson 1999; Inger and Bearhop 2008; Bond and Jones 2009).

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

The specific objectives of this study were to determine the stable isotope ratios of birds wintering at aquaculture facilities and natural freshwater and marine habitats, and estimate what proportion of birds at breeding colonies across eastern North America (from Minnesota to Vermont) wintered at each of these habitats. Based on their position in the Mississippi flyway, we anticipated that breeding colonies in Lake Michigan and Lake Huron would contain a greater proportion of cormorants wintering in aquaculture habitats in comparison to colonies to the west or east (Dolbeer 1991, Hatch and Weseloh 1999, King et al. 2010, Scherr et al. 2010).

STUDY AREA

We collected samples at 3 wintering and 5 breeding locations (Fig. 1). Winter locations included Frog Leg Lake (33.544 N, -90.291 W) in the delta region of Mississippi, USA, Lake Guntersville (34.552 N, -86.116 W) in northern

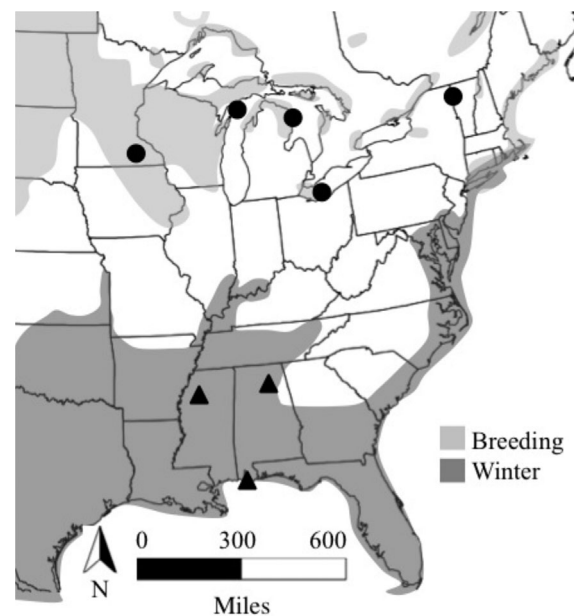


Figure 1. Sampling locations of double-crested cormorants at 3 winter locations (triangles; Frog Leg Lake, Mississippi; Cat Island, Alabama; Lake Guntersville, Alabama) and 5 breeding locations (circles; Wells Lake, Minnesota; Lake Michigan, Michigan; Lake Huron, Michigan; Lake Erie, Ohio; Lake Champlain, Vermont) across eastern North America from 2010 to 2012 (range map adapted from Hatch and Weseloh 1999).

Alabama, USA, and Cat Island (30.316 N, -88.206 W), in coastal Alabama, USA. These locations were chosen for their abundance of aquaculture, natural freshwater, and marine foraging habitat, respectively. Breeding locations were limited to the United States for permitting reasons, and ranged from Minnesota to Vermont, and included Wells Lake (44.291 N, -93.342 W) in southern Minnesota, USA, Garden Bay (45.780 N, -86.577 W) in northern Lake Michigan, Michigan, USA, Thunder Bay (44.999 N, -83.361 W) in western Lake Huron, Michigan, USA, Turning Point Island (41.457 N, -82.727 W) in southwest Lake Erie, Ohio, USA, and Young Island (44.740 N, -73.345 W) in Lake Champlain, Vermont, USA. These locations were chosen to span the cormorant breeding range in eastern North America, and because each had active cormorant management programs from which culled birds could be collected.

METHODS

During January and February of 2011 and 2012, we collected cormorants culled during management activities from aquaculture (Frog Leg Lake; $n = 20$), natural freshwater (Lake Guntersville; $n = 22$), and marine (Cat Island; $n = 19$) winter habitats. We collected growing flight feathers with an active blood supply, and when present, nuptial plumes from each bird and stored feathers in paper envelopes. Growing flight feathers and nuptial plumes were grown in late winter and therefore incorporated the bird's diet during that period.

During April and May of 2010 and 2012, we collected cormorants culled during management activities in Minnesota ($n = 30$), Lake Michigan ($n = 28$), Lake Huron

($n = 30$), Lake Erie ($n = 30$), and Lake Champlain ($n = 20$). We collected nuptial plumes from each bird and stored feathers in envelopes. These nuptial plumes, like those collected on the wintering grounds, were grown in late winter and therefore incorporated the bird's diet during the wintering period. We determined the sex of each bird by dissection. We conducted this research under the approval of Cornell University's Institutional Animal Care and Use Committee (Protocol No. 2001-0091). Samples were salvaged under federal Fish and Wildlife permit MB10621A.

We rinsed feathers with deionized water and dried samples. We analyzed all feathers for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$. We encapsulated a 1-mg sample (± 0.1 mg) of each feather in tin and analyzed it for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a Thermo Finnigan Delta V Advantage isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer (EA-IRMS; Thermo Scientific, Waltham, MA) at Cornell University's Stable Isotope Laboratory. We analyzed an internal laboratory standard of American mink (*Neovison vison*) tissue for every 10 feather samples. We used a chemical methionine standard to measure instrumental accuracy across a gradient of amplitude intensities. We performed isotope corrections using a 2-point normalization (linear regression) of all raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data with 2 additional in-house standards: Cayuga Lake brown trout (*Salmo trutta*) and corn. Based on standard deviations of within-run replicate measurements of standards, we estimated analytical error to be $\pm 0.2\%$ for $\delta^{13}\text{C}$, and $\pm 0.3\%$ for $\delta^{15}\text{N}$. We encapsulated a second 1-mg sample (± 0.1 mg) of each feather in tin and sent it to the University of Utah's Stable Isotope Ratio Facility for Environmental Research for analysis of for $\delta^{34}\text{S}$ using EA-IRMS. Internal laboratory standards were silver sulfide, zinc sulfide and eiderdown and were analyzed for every 10 feather samples. Based on standard deviations of within-run replicate measurements of standards, estimated analytical error was $\pm 0.3\%$ for $\delta^{34}\text{S}$.

We conducted all analyses using the statistical software package JMP (SAS Institute 2012). We compared isotope values of feathers from cormorants wintering in aquaculture, natural freshwater, and marine habitats using an analysis of variance (ANOVA) to confirm that tissues grown in these habitats were isotopically distinct. We then used isotope data from wintering birds to inform a discriminant analysis (Glahn et al. 1995) that identified the winter habitat (i.e., aquaculture, natural freshwater, or marine) of cormorants. First, we used half of the data to inform the discriminant analysis, and then used the second half to test the accuracy of the model. Because the habitat was correctly identified in 100% of the test samples, we then pooled all samples to inform a new discriminant analysis for use in predicting winter foraging habitat in breeding birds.

To confirm that nuptial plumes were representative of the foraging habitats in which wintering birds were collected, we entered stable isotope values of nuptial plumes and growing flight feathers (representing foraging habitat use at the time of collection) from wintering birds into the discriminant model. We observed concurrence between foraging habitat predicted from nuptial plumes and growing flight feathers in

100% of birds. We entered isotope data from breeding cormorant nuptial plumes into the discriminant model to determine the foraging habitat predominantly used during the previous winter. We applied an exclusion threshold of 95% to the posterior probability of membership (Oppel and Powell 2008) to remove individuals from the analysis that used a mix of winter foraging habitats, allowing us to evaluate birds that used only 1 of the 3 focal habitats.

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

RESULTS

Stable isotope values of feathers collected from wintering cormorants exhibited significant variation in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ ($P < 0.001$ for each) among foraging habitats (Table 1). The distribution of sexes was different among wintering environments. Birds sampled from marine environments ($n = 18$) were 100% female, birds sampled from aquaculture environments ($n = 20$) were 90% male and 10% female, and birds sampled from natural freshwater environments ($n = 22$) were 59% male and 41% female. There was no significant difference in stable isotope values between males and females at each location.

For breeding cormorants, we eliminated 10 feather samples from analysis of breeding cormorants because they did not meet the 95% exclusion threshold on the posterior probability of membership to 1 of the 3 habitats. Overall, we sampled 66 males and 62 females. The distribution of winter habitat use varied significantly across breeding colonies ($\chi^2 = 29.7$, $P < 0.001$) and between males and females ($\chi^2 = 20.1$, $P < 0.001$; Fig. 2).

More specifically, the percent of birds wintering in aquaculture habitats varied parabolically with breeding longitude ($P = 0.047$, $R^2 = 0.910$; Fig. 3), increasing from Minnesota (11%, $n = 3$) to the Great Lakes, with a peak in Lake Erie for pooled sexes (43%, $n = 12$; Fig. 3) and a peak in Lake Huron for males (86%, $n = 6$; Fig. 2), then declining towards Lake Champlain (22%, $n = 4$). Of birds that wintered in aquaculture habitats, 82% were breeding in the Great Lakes (Lake Michigan, Lake Huron, and Lake

Table 1. Average (\pm SD) of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values measured in feathers from double-crested cormorants captured on the wintering grounds in aquaculture, natural freshwater, and marine habitats in the southeastern United States during 2011 and 2012. Values of each isotope differed significantly ($P \leq 0.001$) among habitats.

Habitat	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{34}\text{S}$ (‰)
Aquaculture	20	-20.2 ± 1.3	13.0 ± 0.9	0.5 ± 1.5
Freshwater	22	-27.0 ± 1.3	17.3 ± 0.9	3.4 ± 1.2
Marine	19	-19.9 ± 0.6	16.6 ± 0.4	13.2 ± 0.6

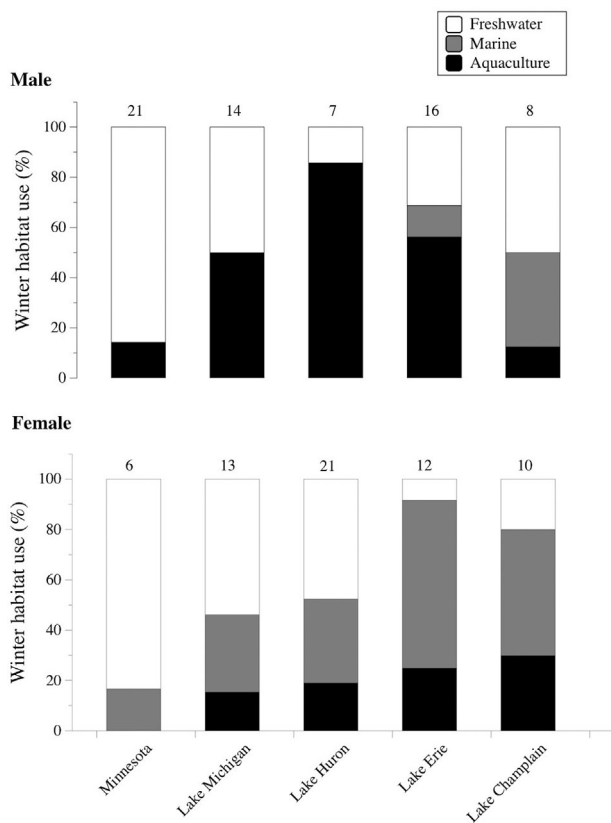


Figure 2. Winter habitat use (% of birds foraging in natural freshwater, marine, or aquaculture habitats, determined using stable isotope analysis of feathers) of male ($n = 66$) and female ($n = 62$) double-crested cormorants breeding across eastern North America from 2010 to 2012. Sample sizes of males and females at each breeding location are indicated above each bar.

Erie combined). From west to east, we also observed a pattern of increasing percent of marine habitat use (from 4% in Minnesota to 40% in Lake Champlain; $P = 0.035$, $R^2 = 0.816$) and decreasing proportion of natural freshwater habitat use (from 85% in Minnesota to 29% in Lake Champlain; $P = 0.197$; Fig. 3).

The proportion of breeding males to females differed significantly among winter habitats ($\chi^2 = 20.1$; $P \leq 0.001$). More males used aquaculture habitats (68% male, $n = 26$; 32% female, $n = 12$), more females used marine habitats (83% female, $n = 25$; 17% male, $n = 5$), and freshwater habitats were used relatively equally by both sexes (42% female, $n = 25$; 58% male, $n = 35$). Males and females also exhibited different patterns in winter habitat use across breeding locations (Fig. 2).

DISCUSSION

This study is the first to provide dietary confirmation of winter resource use in double-crested cormorants breeding across eastern North America. We observed significant variation in winter habitat use. As expected, birds in the Great Lakes (particularly Lake Huron and Lake Erie) had the greatest proportion of aquaculture resource use (representing the peak in the quadratic trend of aquaculture use across breeding longitude), but some proportion of every

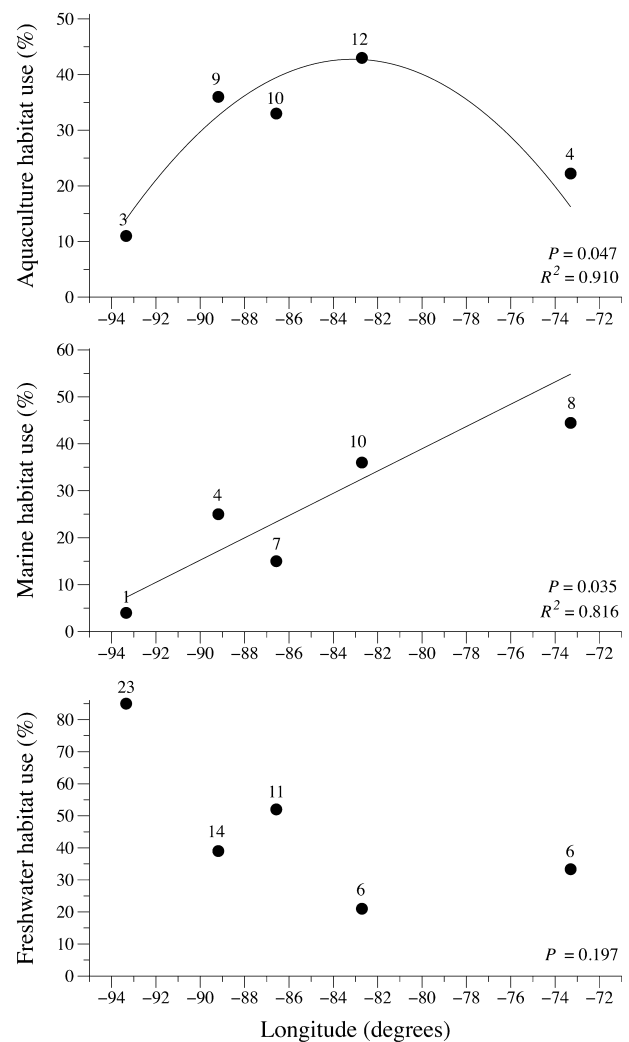


Figure 3. Winter habitat use (% of birds foraging in natural freshwater, marine, or aquaculture habitats, determined using stable isotope analysis of feathers) of double-crested cormorants breeding across eastern North America from 2010 to 2012 (by longitude). Sample sizes at each breeding location are indicated above each point.

breeding colony wintered in aquaculture habitats. This suggests that cormorants foraging in aquaculture habitats are drawn from a broad breeding range (Dolbeer 1991, King et al. 2010). The observed distribution of birds wintering in aquaculture habitats supports the hypothesized division in cormorant migratory routes, with birds breeding in the western Great Lakes using the Mississippi flyway and birds breeding in the eastern Great Lakes towards the Atlantic Coast using the Atlantic flyway (King et al. 2010, Scherr et al. 2010, Guillaumet et al. 2011, King et al. 2012, Chastant et al. 2013). From western to eastern breeding colonies, use of marine winter habitat increased, indicating that coastal environments may be the most critical foraging habitats for birds nesting in the eastern extent of the breeding range. The lack of a significant trend for freshwater habitat use may reflect a lack of longitudinal variation in the availability of freshwater foraging habitats.

Males and females exhibited significant differences in winter habitat use, with a greater proportion of males foraging in

aquaculture habitats and a greater proportion of females foraging in marine habitats. This is clearly supported by the data from both wintering and breeding birds. While sexual segregation clearly occurred in aquaculture and marine habitats, sexes do coexist in natural freshwater areas during the winter (supported by the relatively even distribution of sexes at freshwater overwintering sites, and by the lack of variation in stable isotope values between males and females wintering at these locations). Therefore sexual segregation appears to be limited to birds wintering in aquaculture and marine environments. Sexual segregation in foraging behavior has been observed in other cormorant species (Van Eerden and Munsterman 1995, Bearhop et al. 2006, Quintana et al. 2010), although very few studies of wintering double-crested cormorants have detected it (Glahn et al. 1995). Males, which are the slightly larger sex, may potentially outcompete females for aquaculture habitats with high prey density, and may be better suited to manipulate spiny fish. Alternatively, females may preferentially forage in natural habitats for the greater quality and nutritional value of prey (Nettleton and Exler 1992) and reduced exposure to management activities. While SIA does not provide geographical information about foraging location, we can infer, based on the spatial separation of intensive catfish aquaculture (frequented primarily by males) and marine environments (frequented primarily by females) in the southeastern United States, that male and female cormorants are spatially segregated to a great extent during the winter.

MANAGEMENT IMPLICATIONS

Studies have observed that cormorants wintering in aquaculture habitats primarily breed in the western Great Lakes (Dolbeer 1991, King et al. 2010, Guillaumet et al. 2011, King et al. 2012), making these colonies potential targets for cormorant population management to mitigate aquaculture depredation. However, we observed that colonies across the entire eastern breeding range exhibited a substantial proportion of aquaculture resource use (Fig. 3). For this reason, management of breeding birds in the Great Lakes alone may not alleviate aquaculture depredation because birds breeding farther west and east contribute to the problem, and might contribute increasingly if Great Lakes birds were removed. Furthermore, when employed, the strategy of culling birds on the breeding grounds removes both males and females indiscriminately, and because a significantly greater proportion of males forage in aquaculture habitats than females, this strategy does not effectively target the sex primarily responsible for aquaculture depredation. Together these observations suggest that targeting birds on the breeding grounds is unlikely to be an efficient method for reducing aquaculture depredation by cormorants in the winter. We therefore suggest that focusing management efforts at the site of depredation on the wintering grounds may prove to be a more efficient and effective strategy.

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