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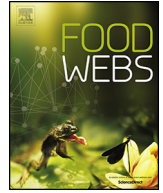
Food habits of wintering double-crested cormorants in the Mississippi Delta

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ABSTRACT

Given its ubiquity, it is not surprising that agriculture, including finfish aquaculture, contributes to food webs worldwide and is used by numerous wildlife for foraging and meeting other needs. Double-crested Cormorants (*Phalacrocorax auritus*) impact United States commercial aquaculture and are considered the primary avian predator in catfish (*Ictalurus* spp.) aquaculture facilities in the Mississippi Delta. Recent changes in aquaculture practices, regulatory policies, and decreased overall hectares in production prompted this study that assessed cormorant consumption of catfish in relation to their night roosts through surveys and diet analysis. Cormorants were collected from night roosts from October through April 2016–2018 ($n = 69$ collections). On average, catfish constituted 33% of a cormorant's overall diet, which is less than reported in previous studies. There was no statistical difference between consumption of channel (*I. punctatus*) and hybrid catfish (*I. punctatus x I. furcatus*) based on biomass estimates, and the greatest consumption of catfish occurred in the months of February and March. The best fit model for predicting catfish consumption was the cubic polynomial function of the area of catfish aquaculture within a 30.6 km forage buffer of a night roost. Our findings will inform wildlife managers about relationships between cormorant night roost locations and consumption of catfish and aid decision making with respect to cormorant management. Despite cormorants having shifted consumption to naturally occurring fish species associated with changes to aquaculture, aquaculture remains an important part of regional food webs.

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1. Introduction

The expansion of agriculture and diminishment of many natural resources is arguably the single most influential anthropogenic caused change to earth's terrestrial and aquatic environments. Half of the world's habitable land is used for agriculture, either livestock or crop production (Ritchie and Roser 2013). Given its prominence on the landscape, it is not surprising that agriculture is used by myriad wildlife for foraging, and agriculture may comprise a major component of food webs worldwide (Mattison and Norris 2005). This use by wildlife in turn can lead to human wildlife conflicts, with astonishing impacts in some cases. It is estimated that pre-harvest losses of rice to rodent consumption in Asia can be as high as 50%, with forgone human consumption in the millions of individuals (Singleton 2003). Impacts are not limited to plant crops, as depredations on livestock occur worldwide and are a highly visible and often controversial component of human

wildlife conflicts (Miller et al. 2016). Typically, this livestock depredation is associated with hooved livestock such as cattle and sheep. However, a rapidly growing source of livestock derived protein is finfish aquaculture, which also is subject to wildlife depredations, particularly from avian predators (Dorr and Taylor 2003). For example, the Double-crested Cormorant (*Phalacrocorax auritus*) caused depredation losses on the catfish (*Ictalurus spp.*) aquaculture industry in Mississippi estimated at $47 million dollars annually (Engle et al. 2020).

The Double-crested Cormorant (hereafter, cormorant) is a large, piscivorous waterbird. Cormorants breed primarily in areas throughout the northern United States, as well as across Canada, and along the Pacific coast up to Alaska. Some populations migrate to winter in habitats along the Gulf of Mexico and the Atlantic Ocean, and along major river corridors. Cormorants are a common overwintering avian species in the Mississippi portion of the Mississippi Alluvial Valley (hereafter Delta). Their population in the Delta grew in the late 20th century, mirroring the expansion of catfish aquaculture in the region (Aderman and Hill 1995). Cormorants are colonial birds that commonly roost in the limbs of trees that overhang water within this region. Bald-cypress (*Taxodium distichum*) and tupelo (*Nyssa spp.*) are common species

that support roost sites in the Delta (Dorr et al., 2014b). Cormorants have been disparaged by many catfish (*Ictalurus spp.*) producers in the Delta because the birds consume commercially grown catfish. A survey completed in 1997 revealed that 77% of Mississippi catfish producers cited cormorants as a source of catfish depredation among wildlife-caused losses (Wywialowski 1999).

Extensive research has investigated cormorant impacts to catfish aquaculture in the Delta. However, many of these studies were conducted prior to or during the peak of catfish aquaculture production in the late 1990s and early 2000s (Stickley et al. 1992, Glahn and Brugger 1995, Glahn and Stickley 1995, Glahn et al. 2000, Glahn and Dorr 2002, Dorr et al. 2012a, Dorr et al. 2012b, Dorr and Engle 2015). Two diet studies were conducted on cormorants in the Delta during this time (Glahn et al. 1995; Glahn et al. 1998). These studies examined the diet of birds that were collected at night roost sites and catfish aquaculture facilities and concluded that cormorants regularly forage fish from aquaculture ponds with ~95% of their diet consisting of catfish and naturally occurring shad (*Dorosoma spp.*). These fish-eating birds consumed on average approximately 0.5 kg of fish per day during winter (Glahn and Brugger 1995).

The catfish industry in the Delta has undergone extensive changes over the past two decades. Catfish aquaculture production in Mississippi peaked in surface area in 2001, with 45,608 ha farmed, but since then, the industry has declined steeply, largely due to increased energy, feed costs, and increased competition from foreign markets (NASS 2002, Bastola and Engle 2012, Dorr et al. 2012a). These factors have contributed to the decrease in total hectares devoted to catfish production in Mississippi by an estimated 68%, which combined with higher stocking densities in the ponds, has resulted in a significant concentration of available fish stock (USDA 2010, Hanson and Sites 2015, NASS 2018). Other changes to the catfish industry in the Delta affecting production have included the culture of a new hybrid species of catfish (*I. punctatus x I. furcatus*), which has a different growth rate compared to previously produced channel catfish and can outgrow the predation size range typical of cormorants more quickly (Li et al. 2004; Dunham and Masser 2012). New aquaculture production techniques are being used that concentrate the catfish into smaller areas, potentially making predation easier (Tucker and Kingsbury 2010).

Recent changes in federal regulations that limit the amount of lethal control aquaculture/wildlife managers can conduct on cormorants have perceived impacts on the amount of catfish being consumed by cormorants (Dorr and Fielder 2017). Currently, wildlife and aquaculture managers disperse cormorants using a variety of non-lethal and lethal measures at night roosts and at catfish ponds. However, managers are spending person-hours dispersing cormorants without knowing the impact the birds have on the catfish industry. Reduced aquaculture pond surface area, combined with a stable wintering cormorant population and the other aforementioned factors, have caused catfish producers and researchers to question how these changes may be influencing foraging behavior of cormorants, such as the possibility of increased exploitation of catfish by cormorants on fewer ponds. These changes necessitate contemporary research to fully understand the effects on cormorant foraging ecology.

In addition to commercial catfish being an important food source for cormorants, other fish species found naturally throughout the Delta are readily consumed by cormorants. Of these natural fish species, shad (*Dorosoma spp.*) is the most often consumed by cormorants and occur in natural water bodies as well as catfish aquaculture ponds although, shad are typically considered undesirable by producers who make efforts to limit their presence (Glahn et al. 1995, Glahn et al. 1998). Other notable natural prey species include freshwater drum (*Aplodinotus grunniens*), sunfish (*Lepomis spp.*), temperate bass (*Morone spp.*), and crappie (*Pomoxis spp.*) that are potentially available as forage for this population of cormorants. Catfish also occur in natural water bodies in the region, however catfish from natural waterbodies typically are not part of the diet of cormorants in other parts of the

country (Glahn et al. 1998, Dorr et al., 2014b); hence, we assumed that all catfish found in the diet originated from aquaculture ponds. Given the potential availability of a diversity of fish species as forage for cormorants, contemporary research was needed on cormorant diets in the Mississippi Delta during winter. Specifically, we sought to: (1) describe the diet of wintering cormorants, (2) examine patterns of catfish consumption by cormorants, and (3) model the relationship between cormorant consumption of the two primary prey species, catfish and shad, as well as other prey species to the area and distance of catfish aquaculture surrounding their night roost sites. We predicted a priori that catfish consumption by cormorants would increase positively with proximity of roost sites to aquaculture ponds.

2. Study area

The Mississippi Delta is an 18,000-km^2 portion of the alluvial plain of the Mississippi River, which encompasses 19 counties in western Mississippi (Pettry and Koos 1980). The Delta contains or is otherwise recognized by rivers such as the Mississippi, Yazoo, and many small tributaries and brakes. Cormorants use the entire Delta for night roosts from October through April annually, and these sites vary in distance from aquaculture facilities and in the amount of nearby aquaculture.

3. Methods

3.1. Cormorant collections

Cormorants were collected from night roosts twice monthly from October through April during winters 2016–17 and 2017–18, coinciding with peak cormorant migration and seasonal residency within the region (Wires et al. 2001; Dorr et al. 2008). A bimonthly aerial survey of all known cormorant night roosts in the Delta was conducted prior to each cormorant collection. During winters 2016–17 and 2017–18, a total of 85 and 79 night roost locations, respectively, from 14 Delta counties were included in each survey (Fig. 1). Six roosts were dropped from flights in year 2 because the roosts had been drained, harvested of timber, or no birds had been observed in those roosts for 3 or more years. Surveys were conducted from sunrise to three hours after and three hours before sunset to last light. This time frame was chosen to count the greatest number of birds while they were at their night roost sites. Numbers of cormorants present in a roost were recorded following procedures established by Arbib (1972) and used as selection criteria for cormorant collections conducted the following evening. Roosts with ≥200 cormorants were identified for inclusion in the pool of sampled sites, which were categorized based on the distance to the nearest catfish aquaculture pond (0-10 km, >10-20 km, and >20 km). These categories were selected based on the results of Tobin et al. (2002) where they examined the proportion of birds that fly a given distance from the night roost to their subsequent day location. For each collection period, three night roost sites, one from each distance category, were randomly selected for collection. If there were no active night roosts in a given distance category for that collection period, another roost from a different distance category was randomly selected. The same night roost could be selected for collection multiple times if it remained active throughout a winter. Normal cormorant dispersal at night roosts continued throughout this study, which likely affected the distribution of cormorants in the Delta.

Multiple teams of two or three people were assigned to a night roost so that all collections could take place concurrently. Collection teams would arrive at their assigned night roost site at least three hours before sunset to harvest cormorants as they returned to their night roost from foraging. Using suppressed 0.22 rifles and 12-gauge shotguns, ten birds were collected from each night roost, totaling 30 birds per collection period. Cormorant carcasses were retrieved immediately after shooting. After retrieval, a tube was placed down the cormorant's esophagus, where 60 ml of chilled phosphate buffered solution was injected into
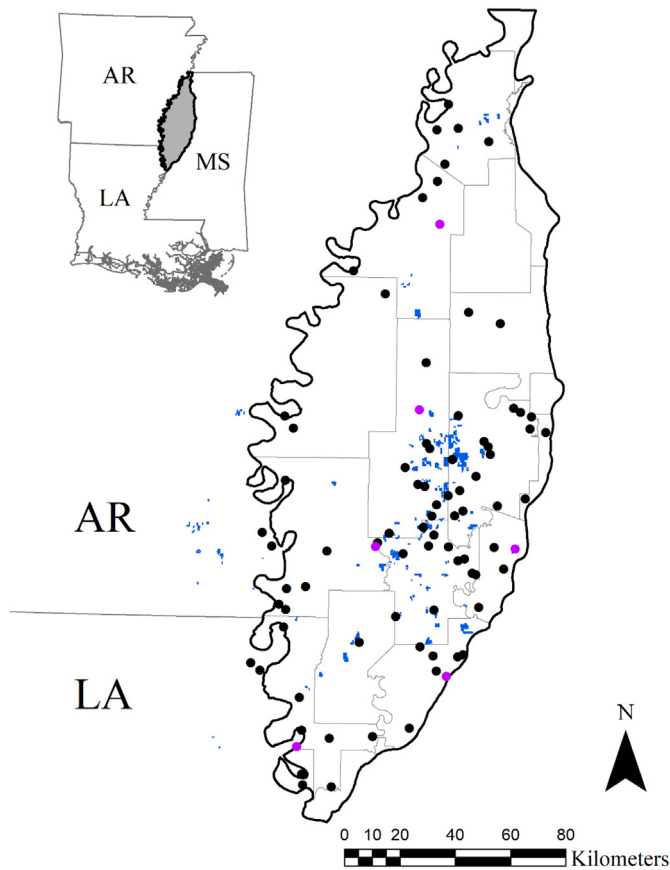
Fig. 1. The Mississippi Delta region and neighboring states of Louisiana and Arkansas with known Double-crested Cormorant night roosts and catfish aquaculture. Black dots signify night roosts surveyed in winters 2016–2017 and 2017–2018, while purple dots signify night roosts surveyed only in winter 2016–2017. Catfish aquaculture that was in production during winter 2017–2018 is represented in blue.

the posterior tip of attachment of the anal fin to the posterior tip of the caudal fin (ANF). For shad specimens (*Dorosoma spp.*), the partial length measurement included the distance from the base of the caudal fin to the posterior point of the caudal fin (CF). For all other species, the distance between the posterior tip of attachment of the anal fin to the posterior tip of the caudal fin (ANF) was measured. Linear regression equations were retrieved from previously published literature or created using a combination of available whole fish samples retrieved from the stomach contents and samples of fish obtained from natural waterbodies in the sample area (Table 1).

Once total length for all fish specimens was derived from regression equations or direct measurement, undigested weights for the fish were calculated using species-specific total length (TL) in mm to weight (W) in g equations retrieved from previously published literature (Table 2). If a fish specimen showed no signs of digestion, a direct weight was obtained rather than using the length-weight relationship equation. When a length-weight equation did not exist for a particular species, an equation from a morphologically similar species within the same genus was used. For catfish specimens that could not be identified to species, an average of the output from length-weight equations was used for all species of catfish found in the study (*I. punctatus, I. furcatus,* and *I. punctatus x I. furcatus*). All catfish were categorized into three distinct size classes that are associated with different catfish aquaculture practices. These include fingerling (total length less than 150 mm), stocker (total length between 150 and 200 mm), and foodfish (total length greater than 200 mm) (NASS 2018, C. R. Engle pers. comm.).

3.2. Statistical analysis

Only cormorants with at least one measurable fish sample in their esophagus/stomach were used for analysis. For the primary analysis, fish specimens were grouped by six taxa that comprised the majority (99%) of prey items in both years and an "other" category for rarely found species. These taxa included catfish (*Ictalurus spp.*), shad (*Dorosoma spp.*), freshwater drum (*Aplodinotus grunniens*), sunfish (*Lepomis spp.*), temperate bass (*Morone spp.*), crappie (*Pomoxis spp.*), and other. Relative prey biomass proportions used in analysis were calculated by determining the relative biomass for each individual bird. The proportions for all birds that were collected from a single night roost during a collection period were then averaged to obtain a prey biomass proportion for that particular roost site and date. These roost biomass proportions were used as the dependent variable for analysis. Relative prey occurrence was calculated using the same procedure as the biomass calculations to compare against each other and to historical findings. Fish specimens determined to be blue catfish (*I. furcatus*) were pooled together with hybrid catfish for analysis as they are not commercially produced in the Delta, and unidentifiable catfish specimens (*Ictalurus* sp.) were proportionally divided between channel and hybrid catfish.

Welch *t*-tests were used to investigate the differences between channel and hybrid catfish consumption, size distribution of catfish, and the effect of cormorant sex on catfish consumption. Data on fish size was evaluated to detect differences in prey size selection among all birds collected and to compare against historical trends in these relationships. To determine if there was a seasonal trend/pattern in catfish consumption, the emmeans package in R version 1.0.136 was used (Lenth 2018). This approach used ANOVA with Tukey's HSD testing to compare means to determine if there was a statistical difference among months.

The betareg package in R was used to build a beta regression model that considered the relative proportion of catfish in a cormorant's diet as the dependent variable, based on its night roost location (Cribari-Neto and Zeileis 2010). To account for 0 s and 1 s in the data, a transformation function was applied to the catfish diet proportion data that uniformly altered the proportions so that 0 s and 1 s did not occur in the data, following the procedure described by Smithson and Verkuilen (2006). The

the stomach to stop digestion and preserve stomach contents. Once all cormorants were collected from a night roost, the birds were labeled and stored on ice as they were transported to a necropsy lab.

Once in the necropsy lab at the United States Department of Agriculture (USDA), Wildlife Services (WS), National Wildlife Research Center (NWRC) Mississippi Field Station, each bird received a unique numeric identifier for storage and subsequent analysis. The cormorants were dissected so that the entire esophagus and stomach could be removed together to minimize the chance of missing stomach content samples. Once removed, cormorant stomachs were placed in individually labeled plastic bags and frozen until later analysis. The sex of all birds was determined using visual observations of the gonads (Dorr et al., 2014b). After these data were collected from a cormorant, the carcass was incinerated.

Stomach-esophageal samples were analyzed by thawing and weighing the intact stomach. Thereafter, stomach contents were removed and rinsed in layered 10 mm and 600 μm sieves so contents could be identified to the lowest taxonomic level possible. Undigested fish specimens were weighed to the nearest 0.1 g. Total length was measured to the nearest mm from the mouth to the posterior end of the caudal fin using 200 mm calipers and a 610 mm ruler. With partially digested fish, typically with the head missing, partial length measurements were recorded to use in regression formulas to determine total length (Glahn et al. 1995). For catfish, measurements recorded included the distance between the anterior tip of attachment of the adipose fin and the posterior tip of the caudal fin (ADF), and the distance between

Table 1
Intercept (a) and slope (b) parameters for partial to total length (mm) equations for common cormorant prey species. Equations are separated by genus and partial length measurement used. Fish specimens used for regressions were obtained directly from cormorant stomachs collected in the Mississippi Delta from 2016 to 2018 and additional samples were used from fish obtained throughout Mississippi and Alabama. The standard equation format is (estimated total length) = $a + b *$ (partial length). Equations were previously unavailable for all species, except those marked with an asterisk which were obtained from Glahn et al. (1995).

Species	Partial length measurement[a]	Intercept (a)	Slope (b)	R^2 value	Total length range (mm)^2	n samples obtained[b]
Aplodinotus grunniens	ANF	16.805	2.675	0.9618	158–230	8
Dorosoma spp.[*]	CF	12.642	3.737	0.9222	N/A	N/A
Ictalurus spp.[*]	ADF	−18.717	2.843	0.9583	43–330	N/A
Ictalurus spp.[*]	ANF	8.269	2.858	0.9599	43–330	N/A
Lepomis spp.	ANF	3.4086	2.4756	0.9818	70.9–138.6	14
Pomoxis spp.	ANF	−14.21	3.273	0.9831	77.5–257	35
Morone spp.	ANF	−3.6361	2.9154	0.9873	63.9–200.9	18
Atherinopsidae	ANF	3.0538	2.7722	0.9118	66.1–106.6	24

[a] Distance between the posterior tip of attachment of the anal fin to the posterior tip of the caudal fin (ANF); Distance between the anterior tip of attachment of the adipose fin and the posterior tip of the caudal fin (ADF); Distance from the base of the caudal fin to the posterior point of the caudal fin (CF).
[b] N/A refers to data that was not available from the source.

area of catfish aquaculture surrounding a night roost within multiple forage radii, distance from the night roost to the nearest catfish aquaculture pond, and month of collection were considered as independent variables in the analysis. Because of a limited sample size of roosts and diet data for some ranges in aquaculture area for some months, variation due to month and area were analyzed separately. Multiple forage buffer radii were used for the aquaculture area variable to account for different forage patterns described by King et al. (1995) and Tobin et al. (2002). Orthogonal polynomial trend analyses were run for each variable to determine the polynomial function that best described the data. After the appropriate polynomial function was determined for each variable, all variables were compared using AIC selection criteria to determine the best fit model. Because the relative proportion of shad and other prey were confounded with the relative proportion of catfish in the diet we ran a separate trend analysis of the proportions of shad and other prey on the selected models to highlight the relationship of other primary prey to variables selected in the catfish model. In addition to the best fit model, the minimum distance model is reported because of its management applications that do not require the need to digitize aquaculture shapefiles to run the analysis.

4. Results

In winters 2016–2017 and 2017–2018, we collected 390 and 338 cormorants ($n = 728$), respectively. Of all cormorants collected, 686 (94.2%) had detectable prey items in their stomach-esophagus, and 519 (71.3%) had prey items that were both identifiable and measurable. In winter 2016–2017, 3894 prey items were identified and 1230 were measurable prey specimens included in the analysis. In winter 2017–2018, 7901 prey items were identified, and 3333 were measurable prey specimens that were analyzed. Night roost collections occurred 37 and 34 times across 20 and 22 different night roost locations in winters 2016–2017 and 2017–2018, respectively. For each night roost site, between five and twenty cormorants were collected for stomach content analysis. Two night roost collections were not included in the analysis given the absence of any measurable prey items, leaving 69 night roost collections available for analysis.

Mean relative consumption of catfish, based on biomass of prey specimens, was similar between years (31.8% in 2016–2017 and 34.2% in 2017–2018; $F_{1/67} = 0.0569$, $P = 0.8122$). Thus, all data were pooled across years for the remaining analyses. Based on the biomass of prey specimens, the mean relative diet of a cormorant in the Delta consisted of 57.6% shad, 33% catfish, 3.1% sunfish, 2.5% temperate bass, 2.2% freshwater drum, 1.4% crappie, and 0.2% other. This trend was consistent with results obtained using relative occurrence of prey specimens, with the average cormorant's diet consisting of 55.9% shad, 34.1% catfish, 5% sunfish, 1.6% temperate bass, 1.4% freshwater drum, 1.3% crappie, and 0.8% other and both biomass and occurrence were similar between years (Table 3). A similar pattern of consumption was observed with respect to number of prey species consumed with shad and catfish being the dominant diet items by number (Table 3). A total of 21 different prey species were identified from stomach-esophageal samples in the study (Table 4).

Based on pooled data of the catfish prey specimens identified to the species level, 59% and 41% were hybrid and channel catfishes, respectively. Consumption of the two species did not significantly differ ($t_{122} = -1.86$, $P = 0.0654$; Fig. 2). Catfish size class distributions were similar between the two species ($t_{189} = 0.60$, $P = 0.55$). Channel

Table 2
Total length (L) to weight (W) conversion equations for common cormorant prey species. Equations are applied at the species level when available and if none exists for the individual species, equations from morphologically similar species in the same genus were used. Associated R^2 values and total length ranges used to create the equations are provided when available. All length measurements are in millimeters and weight is expressed in grams.

Species	Conversion equation	R^2 value[b]	Total length range (mm)	Source
Aplodinotus grunniens	$\log_{10}(W) = -5.419 + 3.204*\log_{10}(L)$	N/A	≥100	Blackwell et al. (1995)
Dorosoma spp.	$\log_{10}(W) = -5.376 + 3.17*\log_{10}(L)$	N/A	≥180	Anderson and Neumann (1996)
Ictalurus furcatus	$\log_{10}(W) = -5.33 + 3.10*\log_{10}(L)$	0.97	70–830	Stewart et al. (2009)
Ictalurus hybrid	$W = 0.000017311(L)^{2.868474309}$	0.996	20–240	Brown et al. (2016)
Ictalurus hybrid	$W = 15.559e^{0.00922(L)}$	0.902	173–635	Brown (2010)
Ictalurus punctatus	$\log_e(W) = -2.3773 + 6.2976E^{-2}(L) - 2.2252E^{-4}(L^2) + 3.5392E^{-7}(L^3)$	0.9789	50–240	Steeby (1995)
Ictalurus punctatus	$\log_e(W) = 0.2736 + 2.5646E^{-2}(L) - 3.2983E^{-5}(L^2) + 1.84E^{-8}(L^3)$	0.9885	130–670	Steeby et al. (1991)
Labidesthes sicculus[a]	$W = 6.3503E^{-2} + 7.5002E^{-3}(L) - 7.7338E^{-5}(L^2) + 4.2904E^{-6}(L^3)$	0.87	13–114	Swingle (1965)
Lepomis cyanellus	$\log_{10}(W) = -4.915 + 3.101*\log_{10}(L)$	N/A	≥60	Bister et al. (2000)
Lepomis spp.	$\log_{10}(W) = -5.374 + 3.316*\log_{10}(L)$	N/A	≥80	Anderson and Neumann (1996)
Morone spp.	$\log_{10}(W) = -5.142 + 3.133*\log_{10}(L)$	N/A	≥70	Bister et al. (2000)
Pomoxis spp.	$\log_{10}(W) = -5.642 + 3.332*\log_{10}(L)$	N/A	≥100	Anderson and Neumann (1996)

[a] Conversion equation used for all species in the Atherinopsidae family.
[b] N/A refers to data that was not available from the source.

Table 3

The proportion of the diet calculated from occurrence of available prey fish specimens (O), and biomass of measurable prey fish specimens (Wt) with associated standard error (SE). Cormorants were collected from the Mississippi Delta (n) and separated by winter season and pooled across years, 2016–2017 and 2017–2018.

Prey Species	O	(O) SE	Wt	(Wt) SE
2016–2017 (n = 390)				
Catfish[a]	34.4%	5.45%	31.8%	6.13%
Shad[b]	56.1%	5.02%	60.3%	5.95%
Sunfish[c]	6.1%	1.78%	3.8%	1.64%
Temperate Bass[d]	0.5%	0.29%	1.8%	0.69%
Freshwater Drum[e]	1.1%	0.34%	1.0%	0.50%
Crappie[f]	0.8%	0.38%	1.3%	0.72%
Other	1.0%	0.39%	0.0%	0.02%
2017–2018 (n = 338)				
Catfish[a]	33.7%	6.21%	34.2%	6.50%
Shad[b]	55.6%	6.26%	54.9%	6.43%
Sunfish[c]	3.8%	0.95%	2.3%	0.90%
Temperate Bass[d]	2.7%	1.33%	3.3%	1.49%
Freshwater Drum[e]	1.7%	0.57%	3.5%	1.27%
Crappie[f]	1.9%	0.90%	1.4%	0.84%
Other	0.7%	0.37%	0.4%	0.32%
Pooled (n = 728)				
Catfish[a]	34.1%	4.08%	33.0%	4.43%
Shad[b]	55.9%	3.95%	57.6%	4.36%
Sunfish[c]	5.0%	1.03%	3.1%	0.94%
Temperate Bass[d]	1.6%	0.66%	2.5%	0.81%
Freshwater Drum[e]	1.4%	0.33%	2.2%	0.69%
Crappie[f]	1.3%	0.47%	1.4%	0.55%
Other	0.8%	0.27%	0.2%	0.16%

[a] *Ictalurus spp.*
[b] *Dorsoma spp.*
[c] *Lepomis spp.*
[d] *Morone spp.*
[e] *Aplodinotus grunniens*
[f] *Pomoxis spp.*

Table 4

Prey species in cormorants' stomach-esophageal contents from birds collected in the Delta during winters 2016–2017 and 2017–2018. The occurrence column represents the total number of fish specimens found within the taxa, while the measurable column is the number of fish specimens where a length measurement could be obtained. Average total length ($\overline{TL}$) and estimated average weight before consumption ($\overline{Wt.}$) are given for each taxa with associated standard error (SE).

Species	Occurrence	Measurable	$\overline{TL}$	SE	$\overline{Wt.}$	SE
Atherinopsidae	59	47				
Labidesthes sicculus	1	1	77.7	–	2.2	–
Menidia beryllina	52	45	86.3	1.9	2.9	0.2
Centrarchidae	441	80				
Ambloplites sp.	1	0	–	–	–	–
Lepomis cyanellus	3	2	99.6	6.1	17.7	2.0
Lepomis humilis	6	3	69.9	4.7	5.7	1.2
Lepomis macrochirus	28	24	96.3	8.8	30.1	8.5
Lepomis sp.	340	41	85.6	7.2	25.2	8.0
Pomoxis annularis	5	4	239.5	15.3	202.2	39.9
Pomoxis nigromaculatus	1	0	–	–	–	–
Pomoxis sp.	55	6	133.8	25.6	52.6	35.5
Cichlidae	4	0				
Oreochromis sp.	4	0	–	–	–	–
Clupeidae	9849	3956				
Dorosoma cepedianum	2683	2432	78.6	0.7	7.7	0.4
Dorosoma pentenense	332	311	69.9	0.7	3.2	0.1
Dorosoma sp.	6834	1213	95.8	1.2	15	0.7
Cyprinidae	1	0				
Ictaluridae	1225	417				
Ameiurus melas	1	0	–	–	–	–
Ictalurus furcatus	16	16	205.4	15.6	87.9	17.4
Ictalurus hybrid	178	172	200.3	3.6	80.8	4.0
Ictalurus punctatus	130	115	203.4	5.7	91.6	7.4
Ictalurus sp.	900	114	203.8	5.1	85.9	6.7
Lepisosteidae	1	0				
Lepisosteus sp.	1	0	–	–	–	–
Moronidae	121	35				
Morone mississippiensis	118	34	157.4	6.9	65.9	8.1
Morone saxatilis	1	1	260.8	–	268.1	–
Morone sp.	2	0	–	–	–	–
Poeciliidae	1	1				
Gambusia sp.	1	1	34.9	–	–	–
Sciaenidae	84	23				
Aplodinotus grunniens	84	23	208.5	16.3	150.2	26.4
Unidentified Fish	1	0	–	–	–	–
Rocks	4	–	–	–	–	–
Snails[a]	3	–	–	–	–	–

[a] Shells from the Hygrophila clade in the class Gasropod.

catfish ranged from 29.4 mm to 363.4 mm in total length and averaged 203.4 mm (±5.7 SE; n = 115), while hybrid catfish total lengths ranged from 102.3 to 299 mm and averaged 200.3 mm (±3.6 SE; n = 172; Table 4). Fingerlings, stockers, and foodfish comprised 16.4%, 32.8%, and 50.8%, respectively. Pooled across years, catfish consumption was skewed toward male cormorants. Male birds constituted 51% of the total birds collected, but they consumed 77% of the total catfish biomass between the sexes. Male cormorants had greater proportions of channel catfish (t_{473} = 3.36, P = 0.0008) and hybrid catfish (t_{485} = 4.07, P = 5.4e-05) in their diet compared to female birds.

Proportions of catfish in cormorant diets varied throughout the winter (Fig. 3). There was no difference (P > 0.05) in proportions of catfish consumed in October through January, where monthly means were 24.11% (± 8.79% CI), 20.02% (± 7.12% CI), 21.56% (± 8.35% CI), and 23.52% (± 7.31% CI), respectively. Catfish consumption during February and March ($\overline{x}$ = 48.33% ± 9.92% CI; $\overline{x}$ = 67.48% ± 9.64% CI) was significantly higher (P < 0.05) than October through January; however, consumption for those months did not differ (P > 0.05) between each other or with April. Consumption during April ($\overline{x}$ = 48.32% ± 14.87% CI) was only significantly higher (P < 0.05) than November and December.

Beta regression models were used to represent the proportion of catfish, shad, and other prey in a cormorant's diet. The catfish model that was selected as the best fit by AIC selection criteria was the cubic polynomial function of area of aquaculture within a 30.6 km forage radius of the night roost (P < 0.0001, Pseudo R^2 = 0. 4572; Fig. 4). Shad and "other" prey species models were included in the 30.6 km area model and were cubic and linear functions with pseudo R^2s of 0.3445 and 0.0928, respectively (Fig. 4). The next best model was not competing and had a ΔAIC of 3.2287 (Table 5). The best fit model for catfish consumption using the minimum distance to the nearest aquaculture pond was a quadratic polynomial function of the distance in km (P < 0.0001, Pseudo R^2 = 0.2805; Fig. 5). Shad and "Other" prey species

models were included in the distance model and were quadratic and cubic functions with pseudo R^2s of 0.2286 and 0.0991, respectively (Fig. 5).

5. Discussion

Agriculture is a significant contributor to food webs worldwide and aquaculture in the Mississippi Delta is no exception. Despite recent changes in farmed area, production methods, and catfish species produced the food habits and foraging dynamics of cormorants are influenced by surrounding catfish aquaculture in the Delta. While there has been a substantial decline in catfish aquaculture, and a shift in cormorant diet to non-cultured prey, clearly aquaculture remains an important contributor to the regional food web. Overall, we found that cormorant diets contained a similar variety of species to previous studies in 1989–1991 (Glahn et al. 1995). However, catfish constituted a smaller overall biomass proportion of the diet (33%) than previously reported (50%). We found that cormorants consumed the newly cultivated hybrid catfish in similar amounts to the traditionally produced channel catfish. In this study, the average size of catfish consumed was similar between the two species of catfish, but these fish (202 mm total length) were larger than the average sized catfish consumed in Glahn et al. (1995) (169 mm total length). The distribution
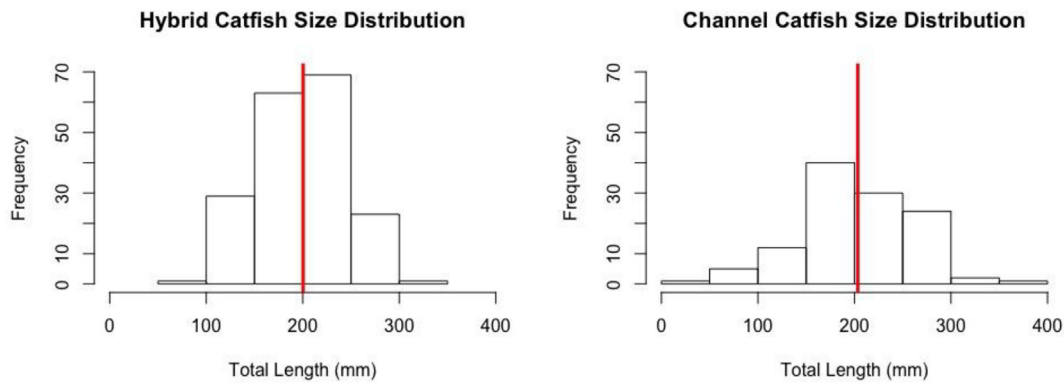
Fig. 2. Size class distributions for catfish prey specimens found in cormorant stomach-esophageal tracts from birds collected at night roosts in the Mississippi Delta, during winters 2016–2017 and 2017–2018. Red bars represent the means of 200.3 mm and 203.4 mm for hybrid and channel catfish, respectively.
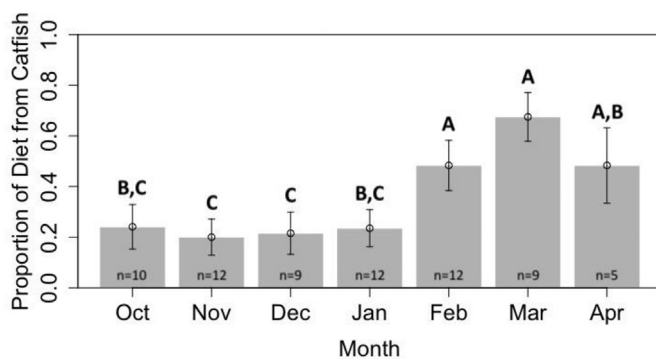

Fig. 3. Mean proportion of a cormorant's diet consisting of catfish and 95% confidence limits for birds collected from the Mississippi Delta, pooled across winters 2016–2018. Letters represent Tukey's HSD test results for determining significant differences and (n) represents the number of roosts that cormorants were collected from during each month.

of prey size covered three catfish production size classes including fingerling, stocker, and foodfish. This consumption range demonstrates that cormorants forage on fingerling and foodfish ponds regardless of species being produced. We detected a similar seasonal shift in the diet of cormorants relative to their consumption of catfish as reported previously (Glahn et al. 1995). Our study is the first to measure the spatial relationship between cormorant night roosts and aquaculture ponds, as well as the total area of aquaculture surrounding cormorant roosts as related to diet.

Using the prey biomass or occurrence metrics to calculate the diet proportions resulted in similar outcomes. To remain consistent across studies, we used the biomass calculations so that our results could be compared to the findings of Glahn et al. (1995). The primary prey species diversity identified in the cormorant diet in this study are similar to those found in historic diet studies conducted in the region, with shad and catfish constituting most (~90%) of the prey (Glahn et al. 1995; Glahn et al. 1998). However, the proportions in which the fish species were consumed have changed. Glahn et al. (1995) found that, on average, 50% and 42% of a cormorant's diet consisted of catfish and shad, respectively, while the proportions in our study were 33% catfish and 58% shad. Similar to Glahn et al. (1995), we also observed that male cormorants consume more catfish than females. It has been hypothesized that the larger male cormorants are better able to capture and consume catfish, which possess spines, than females which consume more shad which tend to be smaller and do not have spines (Dorr et al., 2014a). There were other prey species found that included some sport fish, but these comprised a small proportion of the overall

diet (<10%) and were most likely consumed opportunistically. Shad have become the dominant prey source for cormorants foraging in the Delta. An increase in shad consumption is evident in our model when there is less aquaculture surrounding a cormorant night roost (Fig. 4). This relationship supports the hypothesis that as catfish production area has declined over time in the Delta, cormorants in the region have shifted their foraging patterns to naturally occurring prey species.

These results might suggest that cormorant impacts to catfish aquaculture are declining. However, the decline in catfish aquaculture might result in greater impacts on individual farmers because predation may be concentrated on fewer ponds that are less dispersed across the landscape or may occur on higher value products like hybrid catfish. Burr et al. (2020a) suggested that cormorant numbers in the region have declined with declining aquaculture but cormorant densities on aquaculture are similar to historical estimates. Regardless, economic loss estimates to the industry are substantial. Using the data presented here and concurrently collected data from other researchers, Engle et al. (2020) estimated that cormorants contributed to $47.2 million worth of direct losses to catfish from predation.

Previous to this study, it was unclear if cormorants consumed the recently cultured hybrid catfish similarly to their historic consumption of commercially produced channel catfish. We found that hybrid catfish did appear in the diet and did not detect a significant difference in the proportions of species being consumed. The average size of catfish consumed between the two species was nearly identical, but their size range did differ. Channel catfish had a larger prey size range compared to hybrid catfish, which we attributed to the fact that hybrid catfish have a faster and more uniform growth rate compared to channel catfish. Improved growth rates in hybrid catfish were thought to deter cormorant predation by reducing the time in which the birds could physically consume the fish. Our findings did not provide a clear answer to this hypothesis. However, we suspect that cormorants key into hybrid ponds when the fish are at optimal sizes and therefore these ponds may have greater predation over a briefer time window compared to channel catfish ponds. Regardless of this change in production species, cormorants continue to predate upon aquaculture ponds and contribute to fish losses.

For the first time, we detected relationships between the area of aquaculture within a given forage radius of a cormorant night roost and its distance to aquaculture relative to a cormorant's diet. Previous studies conducted in the region estimated the likelihood of cormorant predation of catfish aquaculture based on a cormorant's night roost proximity to the Mississippi River but did not address the likelihood of cormorant use of aquaculture with respect to area of production surrounding a roost. The primary diet components of catfish and shad consumption relative to aquaculture mirror each other with catfish consumption increasing with increasing aquaculture area and declining
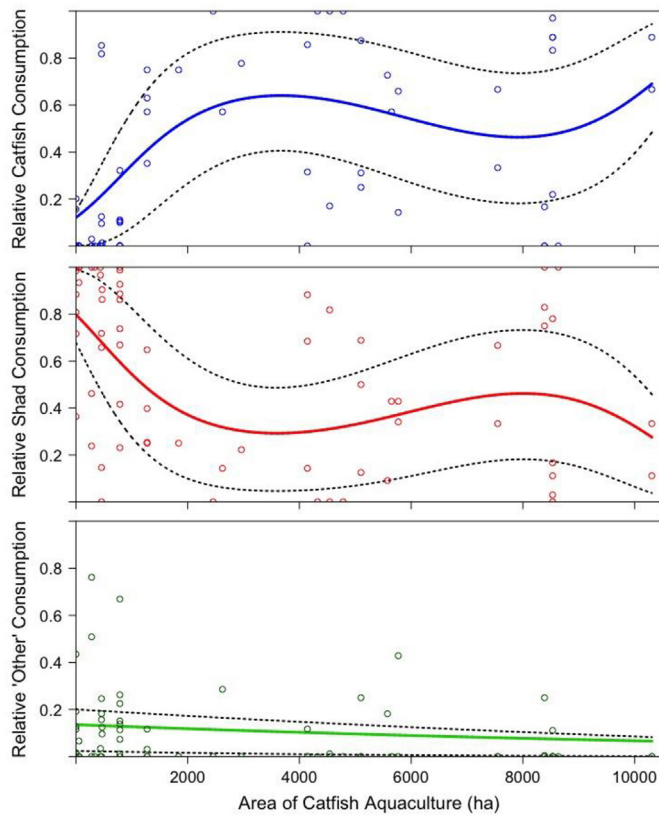
Fig. 4. Predictive model for the proportion of a cormorant's diet consisting of prey species in the Mississippi Delta, based on the area of aquaculture within a 30.6 km forage buffer of the cormorant's night roost location. The average (solid line), 25% and 75% quartiles (dotted lines), and sample data (circles) are shown for catfish (blue), shad (red), and other prey species (green). The following formula is the predicted consumption of catfish by cormorants based on their night roost location: {Logit (Y) = −1.9793 + 1.6487E-03 * (X) - 3.2882E-07 * (X)^2 + 1.8921E-11 * (X)^3}where Y is the proportion of the diet consisting of catfish and X is the area of catfish aquaculture within a 30.6 km forage buffer of the night roost.

Fig. 5. Predictive model for the proportion of a cormorant's diet consisting of prey species in the Mississippi Delta, based on the minimum distance from the night roost to the nearest catfish aquaculture pond. The average (solid line), 25% and 75% quartiles (dotted lines), and sample data (circles) are shown for catfish (blue), shad (red), and other prey species (green). The following formula is the predicted consumption of catfish by cormorants based on their night roost location: {Logit (Y) = 0.4420–0.1399 * (X) + 2.4904E-03 * (X)^2} where Y is the proportion of the diet consisting of catfish and X is the distance from the night roost to the nearest catfish aquaculture pond.

Table 5

Results of Beta regression models predicting the proportion of a cormorant's diet consisting of catfish for birds collected in the Mississippi Delta during winters 2016–2018. Models are polynomial functions of the varying foraging radii of cormorants (King et al. 1995; Tobin et al. 2002).

Radius (km)	Polynomial Function	AIC	Δ AIC	Df	Pseudo R^2
30.6	3	−266.0	0.0	5	0.46
15.7	3	−262.8	3.2	5	0.43
26.3	3	−251.8	14.2	5	0.42
22.2	3	−248.3	17.7	5	0.40
22.1	3	−248.2	17.7	5	0.40
22.8	3	−247.1	18.9	5	0.39
23.4	3	−244.3	21.7	5	0.38
24.4	3	−241.7	24.2	5	0.37
Min Dist[a]	2	−233.0	33.0	4	0.28

[a] The minimum distance from the night roost to catfish aquaculture.

distance from aquaculture facilities; shad, meanwhile, had the opposite relationship (Figs. 4 and 5). "Other" prey species also declined with catfish aquaculture area although the relationship was more linear (Figs. 4 and 5). Examining cormorant diet in relation to the changing landscape has allowed us to better understand the foraging patterns of these birds and in turn provide wildlife and aquaculture managers with improved predation impact estimates.

A goal of this study was to create a predictive model to estimate catfish consumption by cormorants based on the proximity of their roosts to aquaculture ponds. We evaluated minimum distance to the nearest
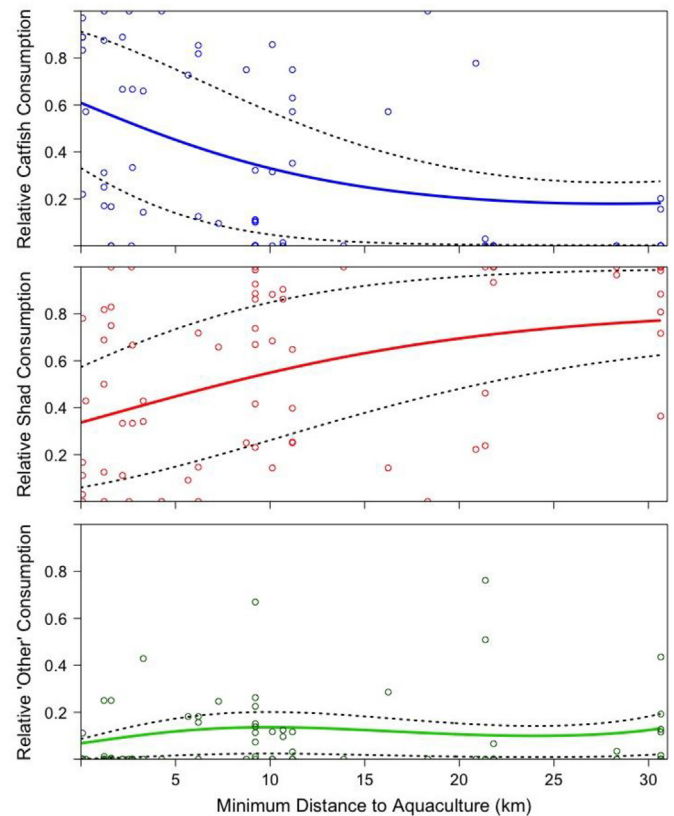
aquaculture ponds and the area of aquaculture within various foraging radii as our explanatory variables in the beta regression model with the best fit model being the cubic function of area of catfish aquaculture within a 30.6 km forage radius. The relationship between catfish consumption and aquaculture area is non-linear, which implies that other factors play a role in cormorant foraging selection outside of aquaculture area alone. Research suggests that cormorants return to the same night roost for several days or more, especially if undisturbed (Tobin et al. 2002). Although central place foraging is typically associated with breeding colonies (Lewis et al., 2001, Dorr et al., 2014a), it is possible the foraging radius described here may represent the limits of distance and energetic tradeoffs for cormorants foraging from a given night roost site (Lewis et al., 2001). In this model, catfish consumption seems to plateau near 3000 ha of aquaculture and begins to increase again after 9000 ha. We note that the second increase may be an artifact of low sample size as we only had two collections from roosts that had greater than 9000 ha of aquaculture (Fig. 4). The plateau could be the result of a food saturation threshold that is met when catfish aquaculture ponds reach a certain level on the landscape. Once the area threshold is met, other factors could be limiting the consumption of catfish, such as inter- and intra-specific competition, handling time of the fish, risk associated with bird dispersal, and amount of natural forage near the roost. This threshold of foraging use hypothesis is supported by Burr et al. (2020a) which showed that while cormorant numbers have declined with declining aquaculture, densities of cormorant on ponds is similar to historical estimates.

We detected a monthly shift in catfish consumption, with the later months having an increased proportion of the diet derived from catfish when we evaluated diet and month alone. However, because of limited monthly sample sizes that did not accurately represent the entire range of aquaculture area, we could not include this effect into our beta regression model. Our data indicated that catfish comprise a larger proportion of the diet in February–April, suggesting that with more data points that cover the entire range of the aquaculture area, these models could be improved by adding month as an explanatory variable. There are multiple hypotheses as to why diet shifts later in the season. One common explanation is that during this time of the year, catfish farmers are moving fish from fingerling ponds to foodfish ponds. At this point, catfish are at the optimal size for consumption by cormorants, and ponds are stocked at high densities with the expectation that some fish will die during the transfer. Another hypothesis is that cormorants undergo hyperphagia before spring migration. This phenomenon is well known in geese (McLandress and Raveling 1981) and postulates that cormorants gorge themselves on a readily available high energy food, like catfish, in preparation for migration energy demands. Evidence supports that cormorants that use aquaculture have higher omental fat reserves, and therefore are in better condition to migrate to their breeding grounds (Glahn et al. 1997).

Using our model, managers can determine which roosts disproportionally contribute to catfish depredation, allowing them to focus dispersal and culling efforts to those sites. Managers can push birds out of roosts where they primarily consume catfish to roosts where the cormorants will switch to natural forage. These natural forage roosts can be used as refuges for the birds, reducing human/wildlife conflict at aquaculture facilities. This model requires the user to digitize and maintain all current aquaculture facilities in the Delta, which is a tedious task that some managers may feel is not as time effective as dispersing birds. As an additional aid, our night roost model (Fig. 5) describing the distance to the nearest catfish aquaculture may also be useful, as this metric is simple and can be performed relatively quickly. By employing this model, a manager can use a common mapping tool like Google Earth™ to quickly determine the distance to the nearest aquaculture facility and estimate the proportion of a cormorant's diet that will consist of catfish. Combining this information with population survey estimates, managers can create a scale of depredation potential per roost and allocate their time dispersing birds at roosts with the greatest potential. While this model uses simpler metrics and is easier to use in practice, the fit according to AIC comparisons was worse than the area model. We recommend that the area model be used in the initial decision-making process of which roosts have the greatest potential for catfish depredation and the associated management of those cormorants.

The predictive power of our model could have been improved with a larger sample size that included a greater seasonal distribution of samples across the gradient of aquaculture surrounding night roosts, allowing for monthly effects to be included in the model. Another form of bias may have been introduced through our collection procedures related to digestion. Birds returning from more distant foraging areas had more time to digest prey items, and our detection of those prey species could be lower than what cormorants actually consumed.

Despite limitations, our study highlights the continued importance of catfish aquaculture to regional food webs and in cormorant diets despite major changes in catfish aquaculture over the last two decades. Burr et al. (2020b) investigated fine scale aspects of catfish aquaculture and environmental factors that influence cormorant foraging selection at catfish ponds. By combining their results with those of this study, managers can better predict where cormorants will contribute disproportionately to catfish losses. This knowledge allows managers to prioritize their time and dispersal efforts to minimize human/wildlife conflicts caused by cormorants predating commercially produced catfish while allowing these native waterbirds to winter in their selected habitat. Cormorants continue to serve as ecosystem indicators in the Delta, sampling the changing prey landscape and providing a measure of the relative effects the catfish aquaculture industry has on local food webs.

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