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Morphometric Variation during Chick Development in Interior Double-crested Cormorants (*Phalacrocorax auritus*)

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Abstract.—In numerous avian species, egg size is correlated to female body condition, hatchling size and nestling growth. Recent demography studies of Interior Double-crested Cormorants (*Phalacrocorax auritus*) suggest a migratory divide across the Great Lakes; western populations winter in the Gulf of Mexico region of the southeastern United States (Alabama, Arkansas, Louisiana, and Mississippi) with extensive catfish (*Ictalurus punctatus*) aquaculture, and eastern populations winter in Florida, where catfish aquaculture is not pervasive. If Double-crested Cormorants have improved their overall body condition through catfish exploitation, then egg and chick sizes should also be affected. Three breeding areas in Ontario (east, central, and west) were selected for empirical measures of size variation. During the breeding seasons of 2006 and 2007, egg, naked young, fledgling, and adult morphometric data were collected. Eggs in eastern areas (volume = $465.8 \pm 3.9 \text{ cm}^3$) were on average larger than eggs in central (volume = $458.1 \pm 3.5 \text{ cm}^3$) and western (volume = $451.7 \pm 3.5 \text{ cm}^3$) areas. However, chicks in eastern areas (culmen = $54.9 \pm 0.6 \text{ mm}$) were smaller than chicks in central (culmen = $57.6 \pm 0.4 \text{ mm}$) and western (culmen = $59.3 \pm 0.3 \text{ mm}$) areas, not only at hatching, but throughout development and fledging. A comprehensive Double-crested Cormorant morphometric gradient that may suggest a potential reproductive advantage for birds exploiting aquaculture facilities is presented. Received 6 July 2015, accepted 26 October 2015.

Key words.—aquaculture, chick development, clutch size, Double-crested Cormorant, egg size, Great Lakes, morphology, *Phalacrocorax auritus*.

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Interior Double-crested Cormorants (*Phalacrocorax auritus*; hereafter, cormorant) have increased throughout much of their breeding range. For example, breeding numbers have increased in the Great Lakes from 89 nests in 1970 to over 115,000 nests in 2000 (Weseloh *et al.* 1995, 2002). During the last 30 years, wintering populations of cormorants in the southeastern United States have also increased, concomitant with growth of the channel catfish (*Ictalurus punctatus*) aquaculture industry in that region (Glahn and Stickley 1995; Glahn *et al.* 1999; King *et al.* 2010). With increased aquaculture, researchers suggest cormorants have shifted their winter range from the Gulf of Mexico coast to encompass these areas of high catfish production (Glahn and Stickley 1995; King *et al.* 2010). Satellite telemetry data revealed the summer ranges of cormorants captured near southeastern aquacul-

ture facilities include the Great Lakes and the Prairie Pothole Region of the Northern Great Plains (King *et al.* 2012). Moreover, King *et al.* (2010) reported a 454% increase in band recoveries from southeastern aquaculture areas compared to a 55% increase in other areas since the mid-1980s. Most (> 90%) of these recoveries were from birds banded as young-of-the-year in Lake Huron, Lake Michigan and Lake of the Woods (King *et al.* 2010).

Across many avian species, female body condition affects egg formation; birds with better body condition typically produce larger eggs (Amundsen and Stokland 1990; Chastel *et al.* 1995; Bernardo 1996). Egg size is also positively correlated to hatchling size, nestling growth and overall progeny fitness in many species (Williams 1994; Christians 2002). At commercial aquaculture facilities, cormorant numbers peak in March, before

spring migration, and catfish comprises 87% of their diet (Glahn *et al.* 1999). These piscivorous birds have subsequently increased their overwinter survival by improving body condition through catfish exploitation (Glahn *et al.* 1999; Chastant *et al.* 2014). Using sulfur isotope analysis from feathers grown during winter months, Hebert *et al.* (2008) also suggested that if cormorants spent at least a portion of the winter foraging at aquaculture facilities, they returned to the breeding grounds in better physical condition than cormorants that solely fed in marine environments.

A recent study of cormorant movement suggests the Appalachian Mountains may serve as a migratory divide for cormorants across the Great Lakes; western populations migrate to winter in the Gulf of Mexico region of the southeastern United States (Alabama, Arkansas, Louisiana, and Mississippi), and eastern populations overwinter in Florida (Guillaumet *et al.* 2011). Moreover, population models reveal survival disparity within the cormorant's range; first-year survival rates in western populations more than double the first-year survival rates of their eastern counterparts (Chastant *et al.* 2014). If overwinter foraging on aquaculture facilities enhances body condition of western cormorants, and distinct eastern and western populations truly exist and are differentiable, we predict that reproductive performance of western cormorants will exceed that of the eastern population.

Currently, cormorant chick development has only been recorded for the eastern portion of the Interior range (Dunn 1975; DesGranges 1982), and substantial egg size variation exists throughout their breeding range (Mitchell 1977; Hanbidge and Fox 1996). Furthermore, cormorant egg size and chick development data, mostly collected prior to the aquaculture boom of the mid-1980s, were based on small sample sizes at limited spatial scales, and by different investigators (Dorr *et al.* 2014). The objective of this study was to assess a possible reproductive advantage to birds exploiting southeastern aquaculture by measuring eggs and chicks throughout the cormorant's breeding

range. If management actions to alleviate cormorant depredation of aquaculture facilities are to be successful, the populations that exploit the facilities must be identified.

METHODS

Study Area

We selected three cormorant breeding areas across southern Ontario for acquiring morphometrics (Fig. 1). Study areas included: Lake of the Woods (western), near Kenora, in the southwestern corner of Ontario (49° 39' 46.80" N, 94° 30' 25.20" W); North Channel of Lake Huron (central), near Blind River, in south-central Ontario (46° 6' 28.80" N, 83° 1' 33.60" W); and Eastern Lake Ontario (eastern), near Kingston, in the far southeastern corner of Ontario (44° 11' 27.60" N, 76° 32' 34.80" W). Each of these areas consisted of ground nesting cormorant colonies on a series of small islands within approximately 15 km of the adjacent city. Islands were composed of granite slabs and/or outcroppings ranging in size from 0.2-3.0 ha. The western breeding area included four islands: Manitou Island, Lemon Island, Island North of Lemon Island, and Guano Rock. The central breeding area consisted of seven islands: West Cousin Island, Fortin Rocks, Hurburt Island, Magazine Island, Doucet Rock, West Island, and Middle Grant Island. The eastern breeding area consisted of three islands: Snake Island, Pigeon Island, and West Brothers Island.

Egg and Chick Sampling

During breeding seasons 2006 and 2007, we visited colonies once monthly from May-July, with a post-fledging visit at the end of the season (September). Clutch size and egg measurement data were taken during first (May) and second (June) visits. Egg measurements included maximum length (*L*) and maximum width (*W*) using dial calipers to the nearest 0.1 mm. We used an equation developed for the European Shag (*P. aristotelis*; Coulson *et al.* 1969), a congener of the cormorant, to calculate egg volume (*EV*):

$$EV = 0.51 \times W^2 \times L$$

Freshly laid cormorant eggs are light blue in color; older eggs become stained with feces and dirt during incubation (Dorr *et al.* 2014). We collected data from freshly laid eggs and classified eggs laid before 1 June as 'early' and eggs laid after 1 June as 'late' (McNeil and L  ger 1987). We stretched a 50-m tape measure in a straight line in a random direction across each colony we sampled. We systematically chose nests (*n* = 60 for each area, both years) in 5-m increments and measured all the eggs in the corresponding nest. We calculated colony clutch size as the average number of eggs per nest for all "Apparently Occupied Nests (AON)" present in the colony (Weseloh *et al.* 1995). To avoid pseudoreplication of the laying female, we used the nest as the independent sample unit.

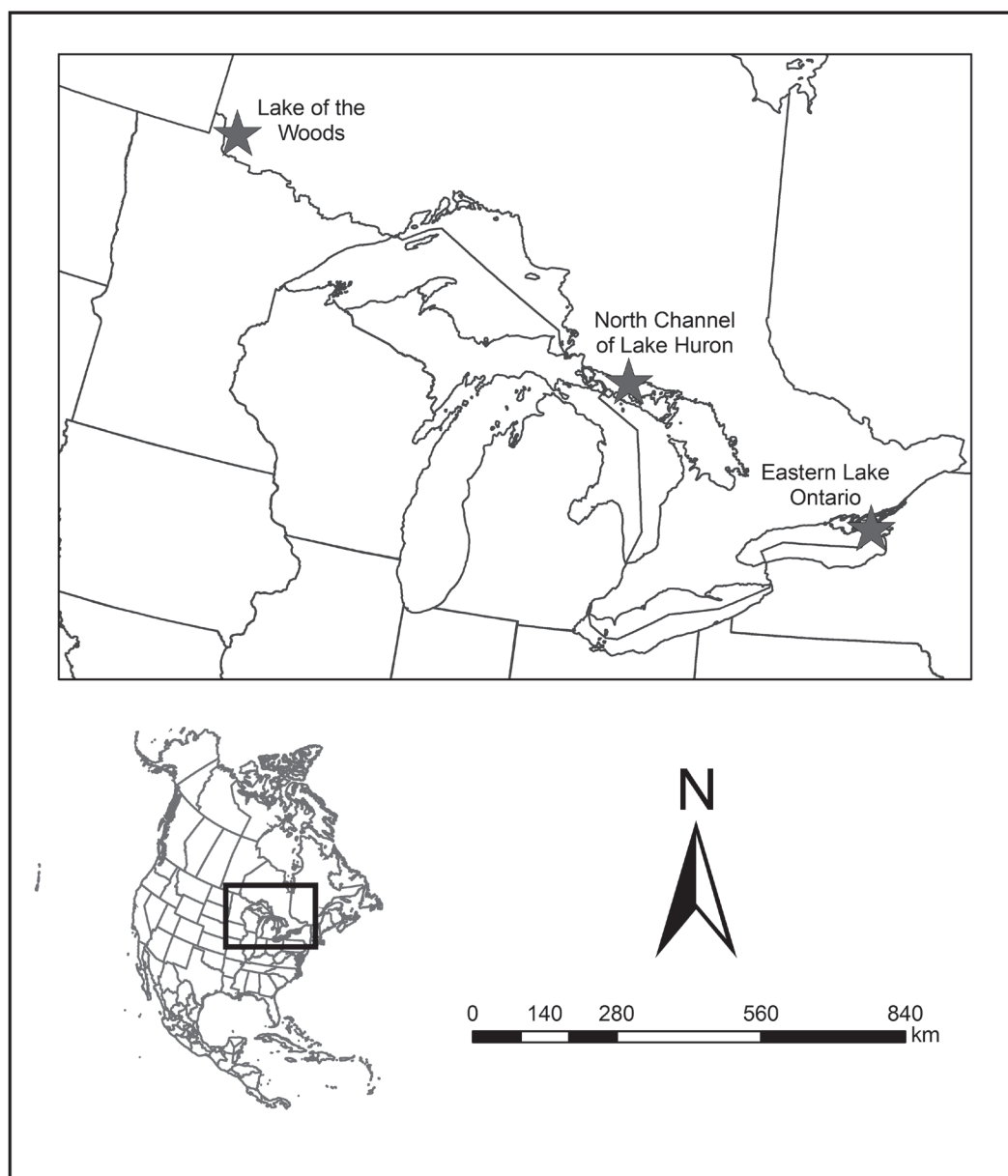


Figure 1. Map of the study area showing the three Interior Double-crested Cormorant (*Phalacrocorax auritus*) breeding areas sampled during summers 2006 and 2007.

Northwestern and upper Great Lakes cormorant colonies initiate nesting 2 to 3 weeks later than colonies in the eastern and lower Great Lakes (Ewins *et al.* 1995). We classified chicks into age groups to account for the observed temporal variation across the large geographic scale. Without regard to gender, we randomly selected and measured naked cormorant chicks (one per nest), and assigned an age class based on their size, skin color ('pink'), egg tooth, and whether or not the eyes were closed or open (3-4 days after hatching but before short down begins to appear in

6-7 days; Dorr *et al.* 2014). Later in the season, we randomly pulled fledglings with ≤ 15 mm of the primary feather sheath present from the crèche and measured them. Morphology measurements included exposed culmen, tarsus, and ulna lengths using dial calipers to the nearest 0.1 mm, flattened wing chord length using a ruler to the nearest mm, and body-mass using a pesola scale to the nearest 0.1 kg. We measured the ulna, flattened wing chord (wrist joint to tip of longest primary), and tarsus (metatarsus from proximal to distal joint) as the greatest length of the segment with the

ruler/calipers held parallel to the bone and adjacent portions of the appendage held at a right angle. We measured exposed culmen from the most distal point of the bill to the notch at the base. We trapped and measured adult cormorants at randomly selected active nests using modified padded leg hold traps (King *et al.* 1998).

Each year during the fledging stage of chick development, we conducted a census on foot of all nests and estimated the number of fledglings in a colony using direct observation. We used a technique modified from Weseloh *et al.* (1995) to estimate colony-specific fledge rates ($CFR = \text{number of fledglings/nest/colony}$) with the following equation:

$$CFR = \frac{Fl}{Tn - An}$$

where Fl is the total number of fledglings in the colony, Tn is the total number of nests, and An is the number of active nests. Given the advanced stage of the breeding season, we assumed active nests containing eggs or naked young did not contribute to the number of fledglings present in the colony at the time of the count (Weseloh *et al.* 1995).

Statistical Analysis

We investigated variation in egg volume, clutch size, and fledge rate among breeding areas using a standard Analysis of Variance (ANOVA) and Fisher's Least Significant Difference pairwise comparisons (SAS Institute, Inc. 2013). We used principal components analysis (Oksanen *et al.* 2011) on the morphological measurements (culmen, tarsus, and flattened wing chord) of chicks, fledglings, and adults to determine body condition; the first principal component (PC1) was a measure of body size. We regressed PC1 against body mass and treated the residuals, the positive or negative difference from an expected body mass for a given body size, as a measure of body condition (Hebert *et al.* 2008; Craig 2015). We then performed ANOVAs and Tukey's Honest Significant Difference tests (R Development Core Team 2014) on body condition for chicks, fledglings, and adults to investigate differences among the three breeding areas. We separated chicks based on their developmental stage (eyes closed vs. eyes open). Statistical significance for all tests was concluded at $\alpha = 0.05$ level.

RESULTS

Egg and Clutch Sizes

We used a total of 885 eggs from 318 cormorant nests to examine differences among breeding areas. Egg volume varied among breeding areas ($F_{2,317} = 3.62$, $P = 0.028$); eggs from the eastern breeding area were larger than eggs from the western breeding area (Table 1). Egg volume in the central breeding area was intermediate to the other two areas. There was no significant difference in egg volume between years ($F_{1,317} = 0.83$, $P = 0.364$) or breeding status ($F_{1,317} = 1.45$, $P = 0.230$); thus, we pooled the data across years and breeding status. Mean clutch size varied among breeding areas ($F_{2,317} = 5.25$, $P = 0.006$) with greater clutch sizes in the eastern and central breeding areas than in the western breeding area (Table 1). Clutch size of early breeders was greater than clutch size of late breeders ($F_{1,317} = 12.79$, $P < 0.001$).

Morphological Development

Morphology of naked chicks varied among breeding areas for both eyes closed ($F_{2,109} = 12.66$, $P < 0.001$) and eyes open ($F_{1,91} = 10.95$, $P = 0.001$) chicks (Table 2; Fig. 2). In both instances, eyes closed and eyes open, chicks were smaller in the east ($P < 0.001$) and larger in the west ($P < 0.001$). We did not collect data for eyes open chicks in the central breeding area (Table 2). Fledgling morphology varied among breeding areas ($F_{2,369} = 39.69$, $P < 0.001$; Table 3; Fig. 2) with significant pairwise differences between west and east ($P < 0.001$), central and east ($P < 0.001$), and central and west

Table 1. Egg measurements (SE) from three breeding areas of Interior Double-crested Cormorants (*Phalacrocorax auritus*) across the southern border of Ontario, summers 2006 and 2007. Clutch size was measured as the average number of eggs/nest. Letters in the same row represent Least Significant Difference codes at the alpha 0.05 level.

Metric	Breeding Area		
	Lake of the Woods	North Channel of Lake Huron	Eastern Lake Ontario
Number of nests	123	90	105
Volume (cm ³)	451.7 (3.5) ^B	458.1 (3.5) ^{A,B}	465.8 (3.9) ^A
Length (mm)	60.4 (0.2)	60.8 (0.3)	61.3 (0.2)
Width (mm)	38.2 (0.1)	38.4 (0.1)	38.6 (0.1)
Clutch size	2.5 (0.1) ^B	2.9 (0.1) ^A	3.0 (0.1) ^A

Table 2. Mean morphologic measurements (SE) of naked Interior Double-crested Cormorant (*Phalacrocorax auritus*) nestlings with eyes closed and eyes open from three breeding areas across the southern border of Ontario, summer 2007.

Metric	Breeding Area					
	Lake of the Woods		North Channel of Lake Huron		Eastern Lake Ontario	
	Eyes Closed	Eyes Open	Eyes Closed	Eyes Open	Eyes Closed	Eyes Open
Number	41	33	10	0	61	60
Culmen (mm)	11.3 (0.2)	15.6 (0.2)	11.7 (0.4)	—	10.3 (0.2)	13.8 (0.3)
Tarsus (mm)	15.8 (0.4)	23.2 (0.3)	15.3 (0.6)	—	15.0 (0.2)	21.5 (0.5)
Ulna (mm)	21.4 (0.3)	31.2 (0.5)	20.4 (0.7)	—	20.0 (0.3)	28.5 (0.8)
Mass (g)	50.3 (2.1)	127.7 (4.3)	43.4 (2.4)	—	46.8 (1.5)	111.3 (5.9)

($P = 0.006$). Lastly, we found no difference among breeding areas for adult cormorant body condition ($F_{2, 173} = 2.17$, $P = 0.117$; Table 3; Fig. 2).

Fledge Rate

We used the annual average fledge rate from a total of 10,556 cormorant nests

to examine differences among breeding areas. Fledge rate varied among areas ($F_{2, 5} = 28.42$, $P = 0.011$); nests from eastern breeding areas fledged more chicks (2.04 ± 0.12 chicks/nest) than nests from central (1.30 ± 0.21 chicks/nest) and western (1.34 ± 0.16 chicks/nest) breeding areas (Table 3).

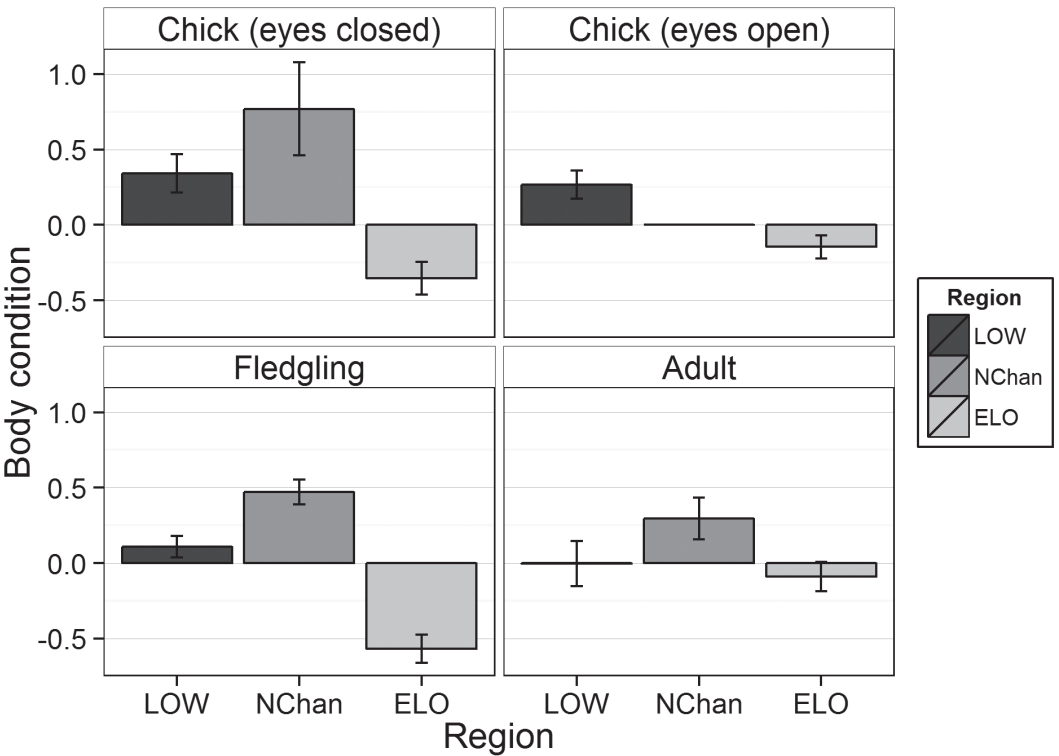


Figure 2. Mean body condition (i.e., residuals of Principal Component 1 regressed against body mass) of Interior Double-crested Cormorant (*Phalacrocorax auritus*) chicks, fledglings, and adults from three breeding areas across the southern border of Ontario, summers 2006-2007. LOW = Lake of the Woods, NChan = North Channel of Lake Huron, and ELO = Eastern Lake Ontario. No data were collected for Eyes Open chicks in NChan.

Table 3. Mean morphologic measurements (SE) of fledgling and adult Interior Double-crested Cormorants (*Phalacrocorax auritus*) from three breeding areas across the southern border of Ontario, summers 2006-2007. Fledge rate was defined as the number of chicks produced per nest, calculated at the colony level and then averaged for each breeding area. Fledge rate was estimated independent from the fledglings used for morphologic measurements (*n*). Letters in the same row represent Least Significant Difference codes at the alpha 0.05 level.

Metric	Breeding Area					
	Lake of the Woods		North Channel of Lake Huron		Eastern Lake Ontario	
	Fledgling	Adult	Fledgling	Adult	Fledgling	Adult
Number	128	32	120	34	125	112
Culmen (mm)	59.3 (0.3)	56.3 (0.4)	57.6 (0.4)	56.3 (0.6)	54.9 (0.6)	58.2 (0.3)
Tarsus (mm)	69.3 (0.2)	68.3 (0.4)	67.6 (0.2)	69.2 (0.3)	67.5 (0.2)	66.5 (0.3)
Ulna (mm)	267.5 (2.1)	328.2 (1.9)	271.1 (2.7)	326.9 (1.6)	230.1 (3.1)	323.5 (1.6)
Mass (g)	1,935.5 (17.5)	2,067.2 (31.2)	1,651.4 (23.0)	2,008.8 (37.9)	1,658.8 (21.6)	2,074.5 (17.1)
Fledge rate	1.3 (0.2) ^B		1.3 (0.2) ^B		2.0 (0.1) ^A	

DISCUSSION

Cormorant egg size and chick morphology varied regionally across their breeding range. Cormorant eggs in the east were larger than those in the west. However, chicks in the east, not only at hatching but throughout development (naked through fledgling), were smaller than the two western breeding areas. But adult cormorants were relatively the same size for all three breeding areas. Our egg measurements were similar to those previously reported for the species (Dorr *et al.* 2014); cormorant egg size increased east to west across North America. Moreover, eggs laid earlier in the breeding season were larger than later-laid eggs, as is common in seabirds (Moreno 1998). It is widely accepted that cormorants do not typically breed until 2 or 3 years of age (Price and Weseloh 1986; Dorr *et al.* 2014). Older, more experienced males arrive at the colony first, selecting the best nesting sites (Siegel-Causey and Hunt 1986; McNeil and L  ger 1987), thus egg volume may reflect the individual's age or level of experience (Christians 2002; Svagelj *et al.* 2015).

Contrary to our expectation, cormorants breeding in western areas, which winter in southeastern catfish aquaculture areas, laid smaller eggs than cormorants breeding in eastern areas, which winter in Florida where catfish aquaculture is not pervasive. Moreover, chick size conflicted with the positive association generally observed between egg volume and nestling

body size (reviewed in Christians 2002; Krist 2011). In this case, the size of naked cormorant chicks increased from west to east (i.e., larger eggs produced smaller chicks). The reason for this anomaly is unknown but likely reflects maternal condition during egg formation. Adult body condition upon arrival at the breeding grounds could result in larger chicks (Hebert *et al.* 2008; Barrionuevo and Frere 2014). The nutrient quality of the yolk sac is likely improved in cormorants wintering near and foraging at aquaculture facilities (Navara and Mendon  a 2008). Also interesting, clutch sizes were smaller in the west despite the perceived better adult body condition. How cormorants allocate resources during egg formation, whether originating from direct food intake and/or from stored body reserves (i.e., capital vs. income breeding; Stephens *et al.* 2009), is unknown. Perhaps females mix breeding strategies by using southern resources as well as local resources to govern egg and clutch size (Bolton *et al.* 1993; B  ty *et al.* 2003). Future study of cormorant eggs using stable isotope ratios is needed to elucidate egg resource allocation (e.g., Hahn *et al.* 2011).

Among altricial species, larger chicks have increased fitness and survival (Ricklefs 1984; Amundsen and Stokland 1990), yet our data show that despite smaller chick size throughout development, fledge rates were greater in the eastern breeding area. Superior foraging opportunities at nest site locations may explain why fledge rate was greater

in the east (Duerr 2007). Larger clutch sizes may also contribute to higher fledge rates, particularly when coupled with superior foraging, because larger clutches facilitate the opportunity to raise more young. Likewise, the cause for reduced fledge rate in western breeding areas is unclear, but may be linked to poor nest site quality or inadequate local foraging opportunities as the birds nesting in the west exhibit weak colony site fidelity (Chastant *et al.* 2014). Colony differences in chick growth and development may reflect age and experience of the adults. DesGranges (1982) found that the most rapid growth rates and largest asymptotic mass came from the oldest colonies where older, more experienced cormorants breed. However, Potts *et al.* (1980) argued that nest site quality had a greater effect on Shag (*P. aristotelis*) fledging success than previous breeding experience. In light of these results, it is unclear whether aquaculture practices provide cormorants with reproductive advantages. At a minimum, we have documented egg and chick development variation within the cormorant's breeding range. Further research is needed to resolve the mechanistic link between winter foraging and cormorant reproduction.

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