

ORIGINAL ARTICLE

Geographic segregation and evidence of density-dependent changes in sex ratios in an abundant colonial waterbird

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Abstract

Demographic information, such as geographic segregation of sexes and sex ratio data, is needed to develop, model and evaluate conservation and management strategies for wildlife. A variety of physiological, behavioral and environmental factors can influence segregation of sexes and sex ratios, many of which originate with density-dependent processes. Departure from 50:50 sex ratios of double-crested cormorants (*Phalacrocorax auritus*) collected during control efforts in breeding and wintering areas across their eastern range of the USA were evaluated using a Z-test as well as Stouffer's weighted Z-tests. In addition, a specifically-designed randomization test was used to evaluate density-dependent effects on primary sex ratios in cormorants from egg collections and colony nest count data over a 21-year period. Cormorants collected from breeding colonies were strongly male-biased, whereas cormorants collected from feeding flocks were slightly biased toward females. Cormorants were partly segregated by sex on the wintering grounds, with significantly more males found in areas with intensive channel catfish aquaculture. The null hypothesis that females produced a balanced sex ratio independent of number of nesting cormorants was rejected: more male embryos were produced during rapid population growth, whereas at maximum nesting number more female embryos were produced. Once populations stabilized, the sex ratio was more equal. This examination of sex ratios indicates that different management methods and locations result in sex-biased culling of cormorants. Sex-biased culling in cormorants could make population reduction efforts more efficient and reduce overall take. We suggest further research to examine density-dependent effects on primary sex ratios documented here.

Key words: Ashmole's halo, management, *Phalacrocorax auritus*, population growth, sex ratio theory

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INTRODUCTION

In wild bird populations, tertiary sex ratios are defined as the sex ratio of breeding adults, but are generally measured as the sex ratio of all non-juvenile individuals (Mayr 1939). Determination of the true tertiary sex

ratio of some avian populations is inherently challenging due to differences in behavior between the sexes, generally higher female mortality, large-scale migration, as well as spatial and temporal segregation of sexes (Van Eerden & Munsterman 1995; Fernandez & Lank 2006; Hebert *et al.* 2008). In a review, Donald (2007) notes that tertiary sex ratios were commonly used as an indicator of population status in the management of some mammals, reptiles and fish populations, but this process has not been significantly developed in the conservation and management of birds.

Primary and secondary sex ratios in birds are defined as the ratio of male to female eggs and chicks, respectively. Sex ratio theory predicts that under specific ecological conditions, the benefits of producing male or female offspring may vary (Hamilton 1967; Trivers & Willard 1973; Charnov 1982; Clark *et al.* 1997). In many cases factors affecting potential allocation of primary sex ratios originate in density-dependent processes. Females have been suggested to facultatively allocate primary sex ratios to avoid competition among their offspring (Hamilton 1967; Clark 1978; Nicolaus *et al.* 2009; Charnov 1982), due to sex-biased offspring dispersal (Hjernquist *et al.* 2009; Guillon & Bottein 2011), and in response to environmental factors that influence parental condition and relative fitness of male and female offspring (Trivers & Willard 1973; Nager *et al.* 1999; Whittingham & Dunn 2000; Pike & Petrie 2005; Nicolaus *et al.* 2009). For example, in avian species for which males are generally larger than females, females in poor condition may produce more female offspring, because male offspring are larger and grow faster requiring greater parental investment (i.e. the 'costly sex hypothesis' [Vedder *et al.* 2005; Nicolaus *et al.* 2009; Pryke *et al.* 2011]).

Detailed demographic information, such as sex ratios, can be useful for conservation and management of bird populations (Donald 2007). For example, research has indicated that manipulation of sex ratios in endangered avian species can be used as a tool for aiding species recovery (Wedekind 2002; Lenz & Wedekind 2007). Conversely, understanding cause and effect of biased sex ratios can be important with respect to species intensively managed due to commercial or subsistence harvest, recreational hunting, or because they are implicated in human-wildlife conflicts (Lercel *et al.* 1999; Collier *et al.* 2007; Donald 2007). For example, Glahn *et al.* (1995) found that male double-crested cormorants [*Phalacrocorax auritus* (Lesson, 1831)] were more likely than females to depredate farmed fish. Bédard *et al.*

(1999) ended a 5-year control program early because male sex-biased culling of cormorants resulted in a faster than predicted reduction in breeding pairs. Through simulation modeling, Collier *et al.* (2007) demonstrated that male-biased brood sex ratio variation causes biologically significant differences in population growth rates of wild turkeys (*Meleagris gallopavo* Linnaeus, 1758). Regardless of goals and objectives, management is most effective when based on fundamental knowledge of ecology, behavior and population dynamics of the species being managed.

The double-crested cormorant is the most numerous and most widely distributed cormorant species in North America (Hatch & Weseloh 1999). Cormorants have generated a great deal of consternation in North America due to real and perceived conflicts with commercial and natural resources such as aquaculture and sport fisheries, their impacts on other colonial-nesting waterbirds, vegetation and habitats (Taylor & Dorr 2003; Rudstam *et al.* 2004; Hebert *et al.* 2005). The Great Lakes population of cormorants increased from fewer than 200 breeding pairs in the mid-1970s to more than 220 000 breeding pairs in the mid-1990s (Hatch 1995), although estimates indicate that the growth rate slowed as the population stabilized in the late 1990s (Wires *et al.* 2001; Weseloh *et al.* 2002).

While the proximate cause of bias in primary sex ratios may be, for example, to avoid competition or to increase mating potential (Hamilton 1967; Clark 1978; Charnov 1982; Hjernquist *et al.* 2009; Nicolaus *et al.* 2009; Guillon & Bottein 2011), the ultimate cause is likely driven by limited resources, and in the case of colonial nesting waterbirds, it may likely be food resources (Lewis *et al.* 2001). Ashmole's halo hypothesis predicts that breeding colony sizes of colonial waterbirds such as the cormorant are regulated by food supply during the breeding season because of prey-depleted halos around colonies (Ashmole 1963). Density-dependent population growth has been documented previously in double-crested cormorants (Ridgway *et al.* 2006) and in the closely related great cormorant [*Phalacrocorax carbo* (Linnaeus, 1758)], in Europe (Frederiksen *et al.* 2001), and is likely based on food limitations (Lack 1966; Birt *et al.* 1987; Martin 1987). Given the declining population growth rates of double-crested cormorants (Wires *et al.* 2001; Weseloh *et al.* 2002), it is reasonable to assume that resource carrying capacity likely has been reached within a large portion of their range at the time of the present study (Weseloh *et al.* 2002; Ridgway *et al.* 2006).

Cormorants east of the Rocky Mountains typically migrate between their breeding grounds in the northern USA and Canada to their wintering grounds in the southern coastal states of the USA (Dolbeer 1991; Guillemet *et al.* 2011), although there are some recently established breeding colonies located in southeastern USA (Hanson *et al.* 2010). To reduce damage to natural resources and aquaculture, cormorants are intensively managed on breeding, migratory and wintering areas. Management of cormorants in the USA and Canada includes both reproductive control by egg-oiling and culling (Bédard *et al.* 1995; Taylor & Dorr 2003; Dorr *et al.* 2012a). Management of cormorants is conducted under the authority of the United States Fish and Wildlife Service (USFWS) and the provincial governments of Canada. In 2003, the USFWS issued a final Environmental Impact Statement (EIS) for the double-crested cormorant in the USA (USFWS 2003). Subsequent to the EIS, management of cormorants during the breeding season intensified, especially in the USA. Since then, the USFWS has identified the need to develop a framework for selecting appropriate management options (USFWS 2009), such as the structured decision-making process (Martin *et al.* 2009), that inherently involves development of simulation models to predict and evaluate the outcome of proposed management scenarios.

Sex ratios are among the most commonly collected statistics for the management of many wildlife game species. However, there is a lack of understanding of the factors regulating sex ratios and segregation of male and female cormorants, and it is not clear how management efforts may affect these demographics in cormorant populations. Predicting the effects of management on cormorant populations may be more accurate when differences in sex ratios are incorporated into modeling efforts (Collier *et al.* 2007). In this study, we examine the tertiary sex ratios of cormorants culled by different methods in eastern USA and describe geographical segregation of male and female cormorants on their wintering grounds in southeastern USA. Additionally, we examine data to test the hypothesis that there are density-dependent effects in primary and secondary sex ratios on cormorant breeding colonies.

MATERIALS AND METHODS

Sampling of cormorants

A total of 1790 adult cormorants were salvaged from breeding colonies, wintering grounds and foraging flocks in Alabama, Arkansas, Michigan, Minneso-

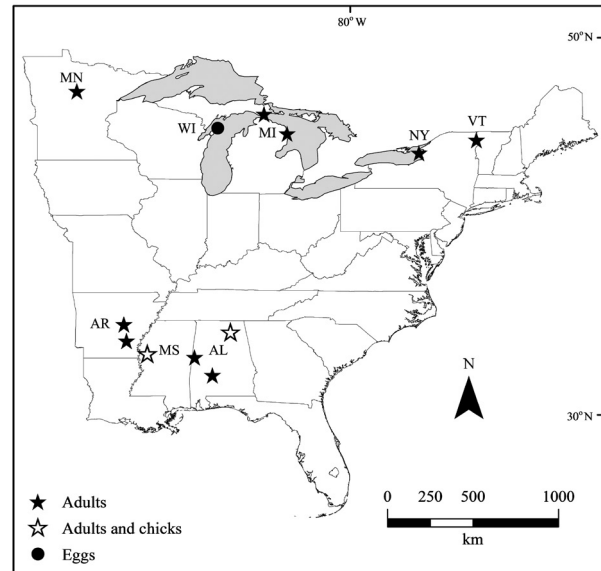


Figure 1 Collection locations of double-crested cormorant adults, chicks or eggs in eastern USA.

ta, Mississippi, New York and Vermont (Fig. 1). Cormorants were collected by United States Department of Agriculture-Wildlife Services (USDA-WS) biologists as part of wildlife damage management control efforts. All cormorants were collected using either .22-caliber rifles or 12-gauge shotguns using a non-toxic shot.

Of the total number of cormorants, 596 were collected from managed breeding colonies from May to Aug 2007 within traditional cormorant breeding ranges in northern USA, and from recently established breeding colonies in southeastern USA in the Delta region of Mississippi (Glahn *et al.* 1995) and Guntersville Lake, Alabama. Cormorants from foraging flocks ($n = 586$) were collected in northern states from May to Aug 2007 and included both breeding and non-breeding cormorants (Custer & Bunck 1992; Hatch & Weseloh 1999).

Wintering cormorants ($n = 608$) were collected from night roosts and directly from aquaculture facilities from Dec 2006 to Mar 2007 and from Nov 2007 to Dec 2007 in Alabama ($n = 180$), Arkansas ($n = 131$) and Mississippi ($n = 179$). We also included an additional 118 cormorants from a separate study (B. Dorr, unpubl. data) that were collected from night roosts in the same region of Mississippi during the winters from 1999 to 2006 (i.e. Mississippi total $n = 297$). Cormorant night roosts on the wintering grounds were considered to be associated

with either natural bodies of water (i.e. major rivers and their oxbow lakes) or aquaculture facilities, according to their proximity to foraging areas (Glahn *et al.* 1995; Dorr *et al.* 2004). All cormorants collected from night roosts in Alabama were located along the Tennessee–Tombigbee and Alabama Rivers. We divided cormorant winter roosts in the Delta region of Mississippi into 2 regions, ‘interior’ and ‘river’ as previously described by Glahn *et al.* (1995). River roosts lie west of US Highway 61 and within 17 km of the Mississippi River. Interior roosts, which lie east of US Highway 61 towards the interior of the state, are located within intensive areas of commercial channel catfish (*Ictalurus punctatus* Rafinesque, 1818) aquaculture facilities and >33 km from the Mississippi River and its oxbow lakes. Cormorants were collected from 3 location types in Arkansas: baitfish aquaculture farms, catfish aquaculture farms, and night roosts located near catfish aquaculture areas. Collected specimens were bagged, labeled and stored frozen until necropsy.

To assess secondary sex ratios, pre-fledged (4–6-week-old) chicks were concurrently salvaged from cormorant control efforts at southern breeding colonies during May–Jun 2007 and 2008 in Mississippi ($n = 40$) and Alabama ($n = 57$) in 2007 (Fig. 1). Collection methods were the same as those used for control efforts of adults, except that chicks were collected from their nests in trees. Sex for all cormorants was determined via necropsy and gonadal examination. Care and use of avian subjects was approved by the USDA-WS National Wildlife Research Center’s Institutional Animal Care and Use Committee (QA-1398).

Sampling cormorant eggs

To determine whether cormorant primary sex ratios may be biased towards males or females, we examined a cache of fertile eggs ($n = 112$) collected from Spider Island, located in Green Bay of Lake Michigan (Fig. 1) and part of the USFWS Gravel Island National Wildlife Refuge. The eggs were collected from cormorant nests in 1988 ($n = 49$), 1996 ($n = 19$) and 2009 ($n = 44$) by USFWS biologists. One egg per nest was randomly collected from a sample of nests that contained ≥ 3 eggs. Eggs were stored frozen until tissue was sampled for sex determination. Eggs were later thawed and a tissue sample from blastodiscs or developing embryos, if present, was dissected and placed in vials containing 95% ethanol. Samples were then shipped to a commercial laboratory (Avian Biotech International, Tallahassee, Florida, USA) for sex determination using dot-blot DNA assays

(Griffiths *et al.* 1998). Biologists with USFWS conducted intermittent cormorant nest counts on Spider Island from 1987 to 2009. We used these numbers to track colony population growth.

Statistical analyses

Tertiary sex ratios

Tertiary sex ratios of salvaged cormorants collected from breeding colonies, from foraging flocks during the breeding season and from the wintering grounds were tested for deviation from parity (50:50) using a Z-test (Freund & Wilson 1997). A combined probability test (Stouffer’s weighted Z; Whitlock 2005) was used to evaluate group deviation from parity.

Primary and secondary sex ratios

We evaluated whether secondary sex ratios observed in chicks from southern breeding colonies and primary sex ratios of eggs collected from Spider Island, Wisconsin were as predicted by processes driven by density-dependent population growth. Because these hypotheses relate to parental fitness as measured by increased survival to sexual maturity of young (Trivers & Willard 1973; Nicolaus *et al.* 2009), bias in sex ratios should be highly correlated in both primary and secondary sex ratios. We hypothesized that when cormorant populations are above carrying capacity, primary sex ratios will be female-biased. In contrast, when populations are below carrying capacity, primary sex ratios will be male-biased. There are 2 primary biological characteristics underlying our density-dependent hypotheses. First, in cormorants, males are generally larger than females (12%–15% by mass; Hatch & Weseloh 1999) and require more parental investment, therefore, breeding females in poor condition due to increased colony size and increasingly limited resources (Ashmole 1963) should produce more female offspring (Trivers & Willard 1973; Nager *et al.* 1999; Whittingham & Dunn 2000; Pike & Petrie 2005; Vedder *et al.* 2005). Second, there should be reduced survival of male young, or they may have below average intrasexual competitive ability or intersexual attractiveness due to limited resources and the greater parental investment needed to raise larger sons (Schjorring 2001; Hjernquist *et al.* 2009). Conversely, when resources are abundant and local populations are below carrying capacity, parents are better able to raise larger males which may have above average intrasexual competitive ability or intersexual attractiveness (Trivers & Willard 1973; Hjernquist *et al.* 2009; Ismar *et al.* 2010). We assumed that the evolutionary stable primary

sex ratio (ESSR [Fisher 1930]) would be 50:50 as there would be no marginal density-dependent advantage to parental investment in either sex when both the local and regional (Weseloh *et al.* 2002; Ridgway *et al.* 2006) cormorant population are at or near carrying capacity.

The 2 southern breeding colonies were considered to be below carrying capacity because they are relatively recently established, are subject to culling and lie in geographic areas that sustain very large overwintering cormorant numbers (Dorr *et al.* 2012b). Cormorant nest counts for each colony demonstrated initial rapid growth in nesting numbers, as expected given that resources are not limited. In addition, culling of cormorants throughout the breeding season was initiated in Mississippi in 2005 and Alabama in 2006, which likely kept breeding cormorant numbers artificially low. We would therefore predict secondary sex ratios to be male-biased. We used Stouffer's weighted Z (Whitlock 2005) to calculate the combined probability that secondary sex ratios in chicks from southern breeding colonies were as predicted by processes driven by density-dependent population growth.

Spider Island primary sex ratios

Primary sex ratios of eggs collected from Spider Island were used to test the underlying hypothesis of density-dependent facultative sex allocation (as described above) cumulatively over all sample periods. We evaluated density dependent growth for the Spider Island colony in 2 ways. First, the mean growth rate in nest numbers was calculated from a recent count (RC), n years after an initial count (IC), using the formula: $[\ln(\text{RC}) - \ln(\text{IC})] / n$ (Weseloh *et al.* 1995) for the periods 1988–1996 (exponential phase) and 1996–2009 (declining phase). Second, a nonlinear regression procedure, SAS PROC NLIN (SAS Institute 2004), was used to fit the observed nest count data to a logistic population growth model (Nelder 1961). The Marquardt iterative algorithm was used for estimation of parameters (SAS Institute 2004; Gumudavelli *et al.* 2007). Convergence criteria were met for the model. The carrying capacity (K) of the system was determined as the asymptote of the fitted model. A pseudo- R^2 was calculated to evaluate the goodness of fit where pseudo- $R^2 = 1 - (\text{SSR} / \text{TSS})$, and SSR is the sum of squares of residuals and TSS is the total sum of squares (Gumudavelli *et al.* 2007; Amarsekare *et al.* 2008).

In 1988, the Spider Island nest count was well below the estimated carrying capacity (Fig. 2) and the Great Lakes population was increasing exponentially (Weseloh

et al. 1995), suggesting that abundant resources were available to breeding females. Accordingly, we assumed that the predicted sex ratio for 1988 was the greatest possible sex ratio (as measured by percentage of males) that can be generated given the observed data (distri_H_0 ; see below). Conversely, in 1996 the nest count was well above the carrying capacity, so the predicted sex ratio for 1996 was taken to be the lowest possible sex ratio given the observed data. Finally, in 2009 the nest count was at carrying capacity, so the predicted sex ratio for 2009 was assumed to be the ESSR (i.e. 50:50; Fisher 1930).

The null hypothesis (H_0) that females produced equal sex ratios independent of nest counts could not be rejected when we tested each year separately using a Z -test. However, this series of independent tests does not sufficiently examine the cumulative probability that the observed sex ratios for each year sampled are as predicted given underlying density-dependent processes (hereafter, H_1). Thus we designed a randomization test, using the software package R, specifically for these data (R Development Core Team 2008; adapted from Guillaumet *et al.* 2010 [see appendix 2]). The euclidian distance (dis_a) to the predicted sex ratio (as predicted above, given H_1) was calculated as:

$$\text{dis}_a = \sqrt{\text{dis}_{1988,a}^2 + \text{dis}_{1996,a}^2 + \text{dis}_{2009,a}^2} \quad (1)$$

where $\text{dis}_{1988,a}$ is the distance of the actual sex ratio in 1988 to the predicted sex ratio in 1988. We next calculated the distribution of the distances (dis_r) to the predicted sex ratio that could be expected when the sex ratios were chosen at random among a set of possible values compatible with H_0 (see Lunneborg 2000). A single value of dis_r was calculated as:

$$\text{dis}_r = \sqrt{\text{dis}_{1988,r}^2 + \text{dis}_{1996,r}^2 + \text{dis}_{2009,r}^2} \quad (2)$$

and a distribution of 10 000 dis_r was generated. If females adjusted their sex ratio in agreement with H_1 , we predict that $\text{dis}_a < \text{dis}_r$, and the P -value of the test corresponds to the number of times where $\text{dis}_r \leq \text{dis}_a$, divided by 10 000 (see Appendix 2 in Guillaumet *et al.* 2010).

We generated the distributions of sex ratios expected under H_0 for each year independently by generating n (sample size) random deviates from a uniform distribution on the interval $[0,1]$, ascribing each deviate as a female if it was ≤ 0.5 , and as a male otherwise, and calculating the percentage of males. This procedure was re-

peated 9999 times, generating a distribution of 9999 sex ratios possible under H_0 , to which we added the actual sex ratio (yielding $distr_H_0$; Lunneborg 2000). Actual distances were then calculated as the number of sex ratios of $distr_H_0$ that were: (i) larger than the actual sex ratio in 1988 (e.g. $dis_{1988,a} = 0$ if the actual sex ratio is larger than any sex ratio generated under H_0 ; $dis_{1988,a} = 1$ if only 1 random sex ratio is larger); (ii) smaller than the actual sex ratio in 1996; and (iii) closer to the predicted (50:50) sex ratio than the actual sex ratio in 2009 (Lunneborg 2000). We calculated $dis_{1988,r}$ in the same way as $dis_{1988,a}$, except that we replaced the actual sex ratio by any possible sex ratio chosen at random from $distr_H_0$ for 1988 (for instance, $dis_{1988,r} = 0$ if the randomly chosen sex ratio is the largest of $distr_H_0$); the same applied to $dis_{1996,r}$ and $dis_{2009,r}$. Significance of all hypothesis tests were assessed using $\alpha = 0.05$.

RESULTS

Tertiary sex ratios: wintering grounds

Cormorants collected from areas of intensive commercial channel catfish production were biased towards males at each location and combined across all locations (78.8%; Table 1). However, cormorants collected near major rivers or at baitfish aquaculture facilities were not biased by sex at each location and combined across all locations (Table 1).

Tertiary sex ratios: breeding grounds

Tertiary sex ratios of cormorants collected from breeding colonies on Lake Champlain, VT and Leech Lake, MN were biased toward males (61.7% and 80.8%, respectively; Table 2). However, sex ratios of cormorants collected concurrently from foraging flocks on either lake were not different ($P > 0.05$) from 50:50. Overall, sex ratios of cormorants collected directly from breeding colonies in all 5 states were biased, resulting in a 68:32 male to female ratio (Table 2). All sex ratios of cormorants collected from breeding colonies were significantly different from 50:50, except those from colonies in Mississippi (Table 2). Overall, average sex ratios of all cormorants collected from feeding flocks during the breeding season were slightly biased toward females (53.6%, Stouffer's weighted $Z = 1.85$, $P = 0.032$; Table 2).

Primary and secondary sex ratios

We did not detect skewed secondary sex ratios in pre-fledged chicks collected from newly established (around 2000) breeding colonies in Mississippi or Alabama (Table 3). However, for all southern breeding colonies combined, we found that secondary sex ratios were male-biased (58.8% males; Stouffer's weighted $Z = 1.66$, $P = 0.048$), as predicted for growing colonies.

Cormorant nest counts on Spider Island indicated rapid population growth during the late 1980s and early 1990s and overshoot in 1995–1997, followed by a pla-

Table 1 Number of cormorants sampled (n), the percentage of males (%), Z -test statistic (Z) and P -value (P) from wintering grounds in non-catfish and catfish aquaculture production areas of Alabama, Arkansas, and Mississippi, USA and combined probability analyses of sex ratios (SWZ) for non-catfish and catfish aquaculture production areas

Location	n	%	Z	P
Catfish aquaculture areas				
Arkansas catfish aquaculture area	33	81.8	3.66	<0.001
Mississippi catfish aquaculture area [†]	227	78.4	8.56	<0.001
SWZ catfish aquaculture areas	2	78.8	4.75	<0.001
Non-catfish aquaculture areas				
Alabama river areas	180	48.3	-0.45	0.326
Arkansas baitfish aquaculture	98	50.0	0.00	0.500
Mississippi River area [‡]	70	42.9	-1.20	0.115
SWZ non-catfish aquaculture areas	3	47.7	0.76	0.223

Sample size (n) for SWZ (Stouffer's weighted Z) is total locations sampled. [†]Eastern region of the Delta region of Mississippi, >33 km from Mississippi River. [‡]Western region of the Delta region of Mississippi, <17 km from Mississippi River.

Table 2 Number of cormorants sampled (*n*), the percentage (%) of males, *Z*-test statistic (*Z*) and *P*-value (*P*) from breeding colonies and foraging flocks from each location and combined probability analyses of sex ratios (SWZ) for breeding colonies and foraging flocks from eastern USA. Sample size (*n*) for SWZ is total locations sampled

Location	<i>n</i>	%	<i>Z</i>	<i>P</i>
Breeding colonies				
Lake Champlain, VT	167	61.7	3.02	0.001
Leech Lake, MN	203	80.8	8.77	<0.001
Little Galloo Island, NY	30	73.3	2.56	0.005
Delta region, MS	63	52.4	0.38	0.352
Lake Guntersville, AL	133	63.2	3.03	0.001
SWZ eastern USA	5	68.1	3.328	<0.001
Foraging flocks				
Lake Champlain, VT	176	48.9	-0.30	0.382
Leech Lake, MN	60	48.3	-0.26	0.397
Thunder Bay, MI	157	51.6	0.40	0.655
St. Martins Island, MI	193	39.4	-2.95	0.002
SWZ Eastern US	4	46.4	1.85	0.032

SWZ, Stouffer's weighted *Z*.

teau and stabilization in subsequent years (Fig. 2). The mean annual growth rate based on nest counts between 1988 and 1996 and between 1996 and 2009 was 29.2% and -2.4%, respectively. The logistic growth rate model was significant ($F_{3,9} = 103.5$, pseudo- $R^2 = 0.83$). Carrying capacity for Spider Island estimated from the logistic growth rate model averaged 2514 nests (95% confidence interval = 2169–2859; Fig. 2).

Observed primary sex ratios at each time period at Spider Island were in agreement with that predicted by density-dependent processes (Fig. 2; 1988 nest count = 332, *n* = 49, % male = 57.1, 1996 nest count = 3340, *n* = 19, % male = 36.8, 2009 nest count = 2503, *n* = 44, % male = 52.3). Likewise, we predicted that the percentage of males of each of the newly-founded southern breeding colonies should be >50%. Again, our results were in agreement with this expectation (Table 3). Based on the results of our randomization test (Fig. 3), the distance of the actual sex ratios to the predicted sex ratios was $dis_a = 3132.73$, whereas the 95% confidence interval for dis_r , the distance to the predicted sex ratios that can be expected at random, was (3608.25–14 373.41). Cu-

Table 3 Number of cormorants sampled (*n*), the percentage (%) of males, *Z*-test statistic (*Z*), and *P*-value (*P*) of pre-fledged cormorant chicks from recently established breeding colonies in Lake Guntersville, Alabama and the Delta region of Mississippi, USA and combined probability analyses of sex ratios (SWZ) for all locations. Sample size (*n*) for SWZ is total locations sampled

Location	<i>n</i>	%	<i>Z</i>	<i>P</i>
Lake Guntersville	57	56.1	0.93	0.176
Delta region	40	62.5	1.58	0.057
Total	2	58.8	1.67	0.048

SWZ, Stouffer's weighted *Z*.

mulative our randomization test thus rejects the null hypothesis ($P < 0.05$) that females produced a balanced sex ratio independently of nest count.

DISCUSSION

Our results indicate that the segregation of male and female cormorants based on habitat type occurs in multiple locations across the wintering grounds. We suggest that geographical segregation of males and females on the wintering grounds is influenced by habitat selection as a result of differences in the prey species available from natural water bodies *versus* catfish aquaculture ponds.

The segregation by sex of inland wintering cormorants has been previously reported only in the Delta region of Mississippi; like Glahn *et al.* (1995), we found a greater percentage of males in night roosts near catfish aquaculture than in roosts near natural water bodies in this region. Previous studies of wintering cormorants found that in the same locations males consumed more channel catfish than females, whereas females consumed more gizzard shad [*Dorosoma cepedianum* (Lesueur, 1818)] than males (Glahn *et al.* 1995). Male cormorants are larger than females, and they can more easily handle and consume catfish from aquaculture ponds, which are larger and possess spines (as opposed to smaller spineless shad). Therefore, males may be better able to utilize the energetically favorable areas associated with intense commercial catfish aquaculture, such as the interior region of the Delta. In contrast, the Mississippi River and its large oxbow lakes provide ample natural foraging habitat and support large schools of shad, which are regularly found in the diet of cormorants foraging in these habitats (Glahn *et al.* 1998).

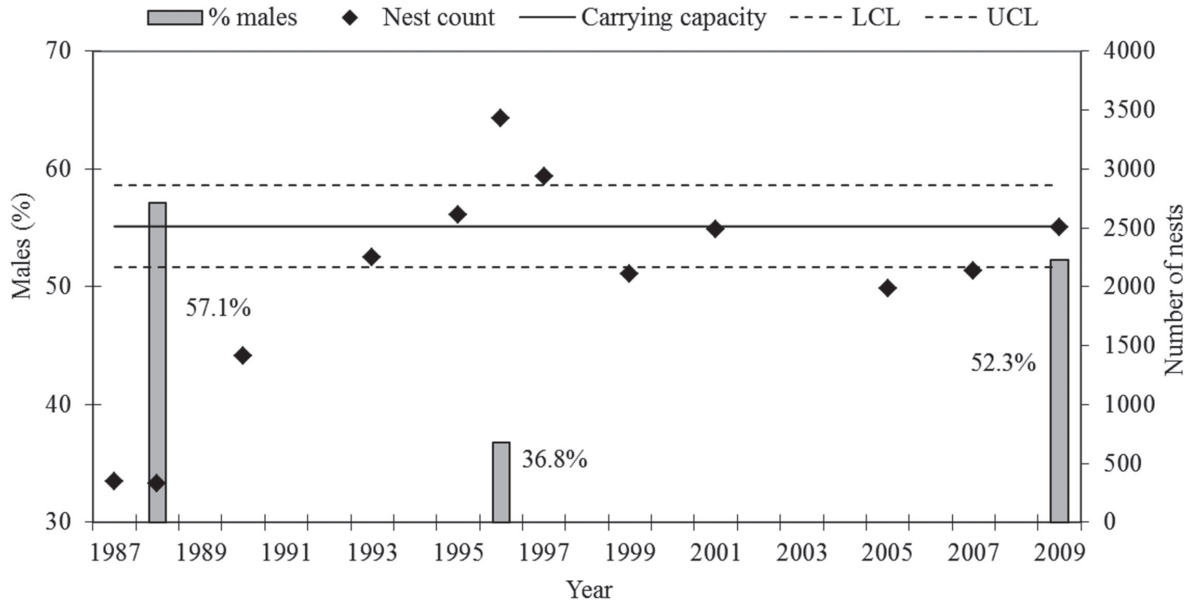


Figure 2 Nest counts, estimated carrying capacity (2514 nests), lower (LCL) and upper (UCL) 95% confidence interval estimates of carrying capacity, and primary sex ratios of double-crested cormorant eggs collected from Spider Island, Lake Michigan, WI in 1988 (nest count = 332, egg sample = 49), 1996 (nest count = 3340, egg sample = 19) and 2009 (nest count = 2503, egg sample = 44).

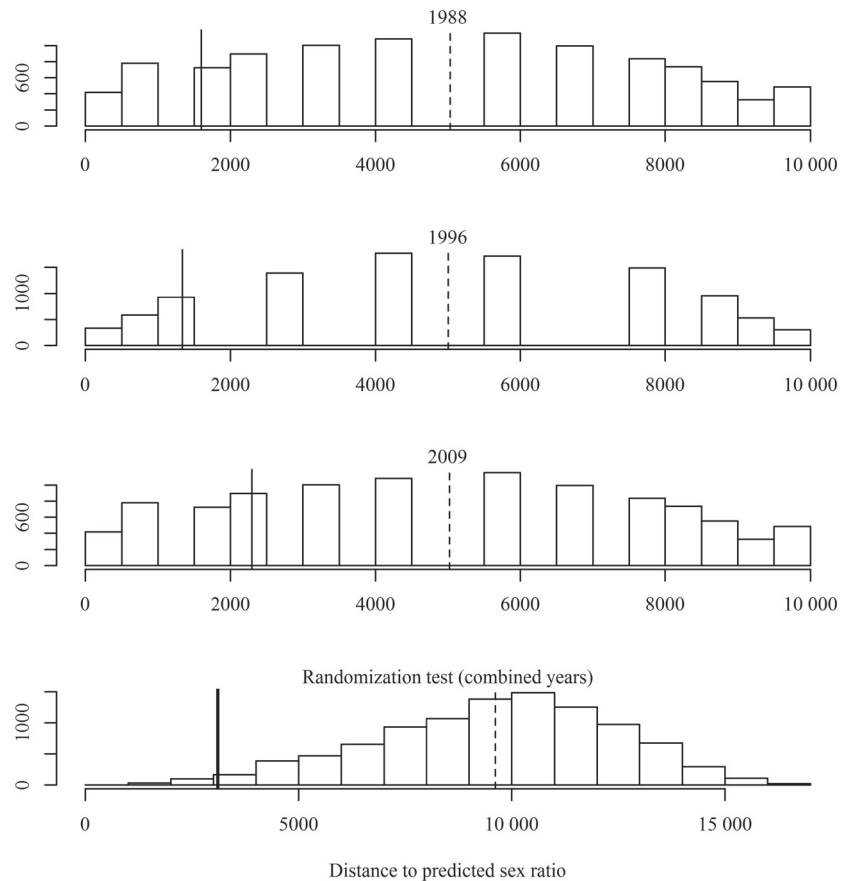


Figure 3 Histograms of the distribution of randomized distances to the predicted sex ratio for each year and all 3 years combined. The mean of the randomized distribution is indicated by a dashed vertical black line, the actual value by a thin solid black line (non-significant, $P > 0.05$, for individual years) or a heavy solid black line (global test significant, see text for details). The discrete nature of randomized distance classes for individual years stems from the discrete nature of possible sex ratios.

In full agreement with this scenario, equal sex ratios also were observed in cormorants collected near rivers in Alabama and from commercial baitfish aquaculture facilities in Arkansas, but were again biased toward males in areas of commercial catfish production in Arkansas. Like the Mississippi River and its oxbow lakes, the rivers of Alabama where cormorants roost provide an ample prey base of *Dorosoma* spp. shad and *Lepomis* spp. sunfish (Mettee *et al.* 1996; Ross 2001). The primary baitfish species of production in Arkansas are golden shiners [*Notemigonus crysoleucas* (Mitchill, 1814)], goldfish [*Carassius auratus* (Linnaeus, 1758)], and fat-head minnows [*Pimephales promelas* (Rafinesque, 1820)] (Wooten & Werner 2004), none of which possess spines; they are all relatively small, and presumably easier to handle and swallow than farmed catfish.

Our results showed that across a wide geographical area, sex ratios of cormorants collected from breeding colonies were heavily biased toward males. Bédard *et al.* (1995) reported similar findings of a 2:1 male to female ratio for cormorants collected from breeding colonies in the St. Lawrence River Estuary. Likewise, Anderson *et al.* (2004) reported that 68% of individuals captured at night from a breeding colony in the Columbia River Estuary were male. We attribute the sex ratio bias to intersexual differences in behavior. Cormorants collected from breeding colonies were continually disturbed during collection activities. As in many avian species, male cormorants typically establish and defend breeding territory (Hatch & Weseloh 1999), and, therefore, may leave nesting areas slower and return quicker than females, thereby exposing themselves to culling and capture to a greater degree than females.

In contrast to culling directly from breeding colonies, overall sex ratios from foraging flock collections were slightly (3.6%) female-biased (Table 2). At locations (VT and MN) where we concurrently had both foraging flock and colony collections, the collections from colonies were significantly male-biased and foraging flocks were not statistically different from 50:50 (Table 2). A different strategy was used when cormorants were collected from foraging flocks than was implemented on breeding colonies. Collections from foraging flocks consisted of targeting individual cormorants while entire flocks passed overhead. These flocks presumably would not be influenced by male-biased territorial behavior associated with the breeding colony and nesting area defense behavior. As a result, males and females likely were exposed to culling to a similar degree when individuals were collected from foraging flocks. It is pos-

sible that other factors such as sex-based differences in activity budgets (e.g. diurnal differences in nest attendance or foraging patterns) could also result in sex-biased culling on the breeding grounds. However, because samples collected from the same local population in the same breeding season differed in sex ratio by method of collection, we think effects of these other factors are unlikely.

This study also provides some evidence for a link between density-dependent breeding colony growth (Ashmole's halo hypothesis [Ashmole 1963]) and maternal allocation of primary sex ratios and parental investment in young. The hypothesis that the growth of the Spider Island colony was density-dependent is supported by trend in colony growth rates and our nonlinear modeling of nest count numbers. The Trivers–Willard hypothesis (Trivers & Willard 1973) predicts that females will modify the sex ratio of their offspring relative to their own maternal condition. In avian species such as cormorants where males are generally larger than females, females in poor condition may produce more female offspring. Although we did not directly measure female body condition of individuals on sampled colonies, previous research provides empirical support that depletion of prey occurs in breeding colonies near or above carrying capacity relative to that during exponential phases of colony growth (Ashmole 1963; Birt *et al.* 1987; Lewis *et al.* 2001) and that local population density can affect maternal condition and provisioning and survival of young (Tella *et al.* 2001; Lewis *et al.* 2006; Moseley *et al.* 2012)

Explanations other than maternal condition (Trivers & Willard 1973) and the 'costly sex hypothesis' (Vedder *et al.* 2005; Nicolaus *et al.* 2009) exist for density-dependent changes in primary and secondary sex ratios. For example, in sexually size-dimorphic species a contradictory theory is that the larger sex has a competitive advantage in intra-brood competition and performs better under adverse conditions ('competitive advantage hypothesis'; see Nicolaus *et al.* 2009). However, in this scenario we would expect to see a reduced or even opposite bias in sex ratio than what was observed in this study. Alternatively, sex-biased natal philopatry and intraspecific competition between males for breeding territory could differentially reduce fitness of male offspring as local population density increases (Schjørring 2001; Hjærnquist *et al.* 2009). Hjærnquist *et al.* (2009) indicated that in species such as cormorants, where males defend territories (Hatch & Weseloh 1999), at low densities and low levels of male–male competition,

females would benefit from producing relatively more sons. Sex-biased dispersal of offspring could also lead to skewed primary sex ratios (Clarke *et al.* 1997; Guillion & Bottein 2011). Sex-biased dispersal in shag and cormorant species has been documented (Aebischer *et al.* 1995; Schjørring 2001), although no clear pattern among sexes is apparent. However, there is no direct evidence of sex-biased natal dispersal in double-crested cormorants.

Our findings are consistent with several of the aforementioned density-dependent hypotheses. We found that more male eggs were produced during the population growth phase at Spider Island and more male chicks in southern breeding colonies; in addition, more female eggs were produced at maximum nesting number, and once populations stabilized, primary sex ratio was almost equal. We recognize that small sample sizes in some data may have affected these results. In addition, there is research that indicates that facultative allocation of sex ratios may not occur at all, at least in some species (Postma *et al.* 2011). Given these caveats, we suggest further research on colony growth and cormorant maternal condition, clutch sex ratios, sex-biased dispersal and fate of young to evaluate possible density-dependent bias in sex ratios in cormorants and other colonial waterbirds. Incorporating molecular analyses and individual fates would be informative to these efforts (Postma *et al.* 2011).

Cormorants are currently managed in both the USA and Canada over much of their range, and future management decisions will be based upon the understanding of how cormorant population demographics are affected by and respond to specific management actions. Based on management goals, this information may be used by managers to target control efforts towards removal of a particular sex. This sex bias may, in fact, make management more effective by reducing the number of cormorants culled to achieve a desired reduction in numbers. Conversely, managers unaware of segregation could unknowingly remove 1 sex disproportionately. Unequal removal of 1 sex more than the other could result in a greater effect on reproductive output of a population if fewer mated pairs are formed in subsequent breeding seasons (Bédard *et al.* 1999; Lercel *et al.* 1999). In addition, greater inter-annual philopatry exhibited by males (Aebischer *et al.* 1995), which may be disproportionately culled, could result in faster than expected declines in breeding colony fidelity or eventual colony abandonment. Alternatively, an increase in young male recruitment to the breeding population may be seen. These

data indicate that managers conducting control work during the breeding season should recognize that males are more susceptible to culling when culling occurs directly from breeding colonies as opposed to foraging flocks. Models to evaluate and predict proposed management plans should also account for these differences.

This study expands on previous research indicating that male and female cormorants are spatially segregated on the wintering grounds due to differences between the sexes in preferences for prey species and availability (Glahn *et al.* 1995). Larger males, which tend to be the primary consumers of commercially raised channel catfish, consume more biomass than females. This difference should be reflected in models predicting impacts to commercial resources, such as consumption of fish biomass in areas where segregation by sex exists.

Carrying capacity of the ecosystem and prey availability may be reflected in local primary sex ratios of cormorants. In our study, the proportion of male eggs varied by as much as 20.3% over 21 years. Lentz *et al.* (2007) indicated that a manipulation of sex ratios of 20% in the endangered lesser kestrel [*Falco naumanni* (Fleischer, 1818)] could significantly affect population size and aid in species recovery. Likewise, Collier *et al.* (2007) did not find significant differences from parity in brood sex ratios of wild turkeys (*Meleagris gallopavo intermedia* Sennett, 1879); however, the average 6.3% male-biased sex ratio difference did produce significant differences in modeled population growth rates.

When cormorant breeding colonies have reached levels beyond their carrying capacity, we may expect more female and fewer male chicks. Culling directly on these same colonies can be expected to result in a higher percentage of males being removed from the local population. Combined, these effects could result in faster than expected declines in breeding pairs due to a shortage of males. However, if management reduces populations below carrying capacity, then we should expect to see more male offspring, which, in turn, are more exposed to culling. These interactions of density-dependent and management effects on sex ratios should be further evaluated and incorporated into future management decisions for double-crested cormorants and investigated in other species of conservation and management concern.

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