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Reproductive Characteristics of Double-crested Cormorants (*Phalacrocorax auritus*) in the Eastern United States: Demographic Information for an Intensely Managed Species

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Abstract.—Double-crested Cormorants (*Phalacrocorax auritus*) are intensely managed through culling in North America to reduce presumed damage to commercial and natural resources. To evaluate this management, there is a critical need to understand the reproductive biology of Double-crested Cormorants. Gonadal development, reproductive potential and breeding status were determined by necropsy for 1,781 Double-crested Cormorants salvaged each month of the year from control programs in their wintering and breeding ranges in seven States in the USA. Gonadal development of males peaked earlier in the year than females. Mean and maximum reproductive potential was five and 13 ovum, respectively. The average proportion of non-breeding female Double-crested Cormorants culled from breeding colonies was 14.9% ($n = 202$) and from foraging flocks on the breeding grounds was 22.1% ($n = 358$). This demographic information should be considered when evaluating and modeling effects of Double-crested Cormorant management in North America. *Received 22 June 2015, accepted 14 August 2015.*

Key words.—breeding status, culling, Double-crested Cormorant, management, nesting colony, *Phalacrocorax auritus*, populations.

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The U.S. Fish and Wildlife Service has implemented two depredation orders (Dorr *et al.* 2012) that allow expanded management of Double-crested Cormorants (*Phalacrocorax auritus*; hereafter cormorant) to reduce local damage to aquaculture and natural resources. This management includes egg oiling, nest and egg destruction, and lethal take of adult cormorants by Federal, State, tribal entities, and their agents on their breeding and wintering grounds (Dorr *et al.* 2014a). Given this intensive management, there is a critical need to understand the reproductive biology of cormorants and the manner in which management efforts affect the cormorant population. Without basic demographic information, we cannot accurately develop population models to evaluate and predict the outcomes of management programs. Our objectives were to describe reproductive potential, determine the timing of development of reproductive organs, and determine the proportions of breeding and non-breeding individuals in local populations to better inform their conservation and management.

METHODS

We salvaged cormorants ($n = 1,781$) that were shot by Federal agency staff as part of control efforts from breeding colonies, wintering grounds, and feeding flocks from December 2006–December 2007 and April 2010 in Alabama, Arkansas, Michigan, Minnesota, Mississippi, New York, and Vermont, USA. Breeding colony collections occurred from May–August 2007 and April 2010. Cormorants were also collected from off-colony feeding flocks in breeding areas in northern States in May–August 2007 and April 2010. Wintering cormorants were collected from December 2006–March 2007 and from November 2007–December 2007. Specimens were stored frozen until necropsy.

We determined sex of all cormorants through visual examination of the gonads. We measured the mass (± 0.001 g) of the left testis of males and the ovary and oviduct of females to determine changes in gonad mass over time. Young-of-year chicks were not measured.

We could not differentiate breeding from non-breeding males based on regression and proliferation of the testis. Females with pre- or post-ovulatory follicles and/or an oviduct with convoluted and striated characteristics were categorized as breeding cormorants, whereas females without pre- or post-ovulatory follicles and a smooth and straight oviduct were categorized as non-breeding cormorants (Dolbeer and Bernhardt 2003). Differences in proportions of non-breeding females at breeding colonies vs. feeding flocks (i.e.,

general population) were determined using a Z-test (Freund and Wilson 1997).

Follicles present on the ovary were categorized as pre- or post-ovulatory follicles. Pre-ovulatory follicles are spherical, contain yolk material, and can be differentiated by size from undeveloped follicles, whereas post-ovulatory follicles are roughly circular, flattened, deflated follicles that have released an ovum through the stigma (Lofts and Murton 1973). The mass (± 0.001 g) of each pre-ovulatory follicle and the diameter (± 0.01 mm) of each post-ovulatory follicle were measured. The number of pre-ovulatory follicles represents the potential number of eggs that could be laid (potential clutch size; Ankney and MacInnes 1978). The number of post-ovulatory follicles was considered the total number of eggs laid during that breeding season. Female cormorants that had an oviducal egg were used to construct pre-ovulatory follicle growth and post-ovulatory follicle regression curves relative to day of ovulation.

Cormorants usually lay eggs daily but may lay every other day (Dorr *et al.* 2014a). The largest post-ovulatory follicle released the ovum in the oviducal egg; therefore, we assumed the egg would have been laid the day after specimen collection. The second largest post-ovulatory follicle represented the egg laid on the morning of the day of collection. Each progressively smaller post-ovulatory follicle corresponded to the ovum released, and egg subsequently laid, during the previous laying interval.

The largest pre-ovulatory follicle represented the egg that would have been laid 2 days after collection, assuming it would ovulate. The second largest pre-ovulatory follicle would have been laid 3 days post collection, and so forth. The weight of the pre-ovulatory follicle on day 0 (the day of ovulation) represented the yolk weight from the oviducal egg. From these measurements, we constructed models of pre-ovulatory follicle progression and post-ovulatory follicle regression relative to day of ovulation. Linear or nonlinear regressions were used depending on model fit as measured by R^2 (SAS Institute, Inc. 2011). For non-linear models, the Marquardt iterative algorithm was used for parameter estimation and pseudo- R^2 was calculated to evaluate the goodness of fit (Gumudavelli *et al.* 2007; SAS Institute, Inc. 2011). Significance of all hypothesis tests were assessed using $\alpha = 0.05$.

RESULTS

We observed changes in average monthly ovary and oviduct mass in female cormorants and left testis mass in male cormorants over time (Fig. 1A). Male gonads developed earlier than females at onset of the breeding season, but female gonads developed more rapidly (Fig. 1A). Male gonadal development peaked in late March to early April, whereas females peaked in May (Fig. 1A).

Forty-three female cormorants had eggs in their oviducts; of these, the average num-

ber of pre-ovulatory follicles observed was 4.81, with a maximum of eight follicles. The average number of post-ovulatory follicles was 2.48, with a maximum was five follicles. Non-linear and linear regression models for pre-and post-ovulatory progression and regression were significant ($F_{2,251} = 1,586.6$, $P < 0.001$, pseudo- $R^2 = 0.76$ and $F_{1,127} = 456.4$, $P < 0.001$, $R^2 = 0.55$, respectively). The models indicated rapid development and regression of post-ovulatory follicles within approximately 7 days (Fig. 1B). Regression equations and the smallest observed post-ovulatory follicle (0.984 mm in diameter) indicated the egg being released from the follicle 7.9 days prior, and the egg laid 6.9 days prior, to collection, or approximately 14 days prior if we assume cormorants lay every other day.

We found that 140 of the 451 breeding female cormorants had ≥ 1 pre- or post-ovulatory follicle present on the ovary. The average number of follicles present on the ovary was 3.5 pre-ovulatory follicles and 1.5 post-ovulatory follicles. The maximum number of follicles observed on any one ovary was eight pre-ovulatory follicles and five post-ovulatory follicles, representing maximum observed reproductive potential.

We found a greater proportion of breeding females was collected directly off the nesting colonies ($n = 202$) than from foraging flocks ($n = 358$) (Table 1). When female cormorants were collected directly off the nesting colonies, 14.9% were non-breeding cormorants. When collected from foraging flocks (away from colonies), 22.1% were non-breeding cormorants. Combined, 19.5% of female cormorants collected during the breeding season (April-August) in this study were non-breeding cormorants.

DISCUSSION

Male gonadal development of cormorants peaked in late March to early April, which corresponds with males arriving earlier on the breeding grounds than females (Dorr *et al.* 2014a). Female gonadal development peaked in late April to early May, suggesting that peak breeding and egg laying for cormorants over much of their breeding

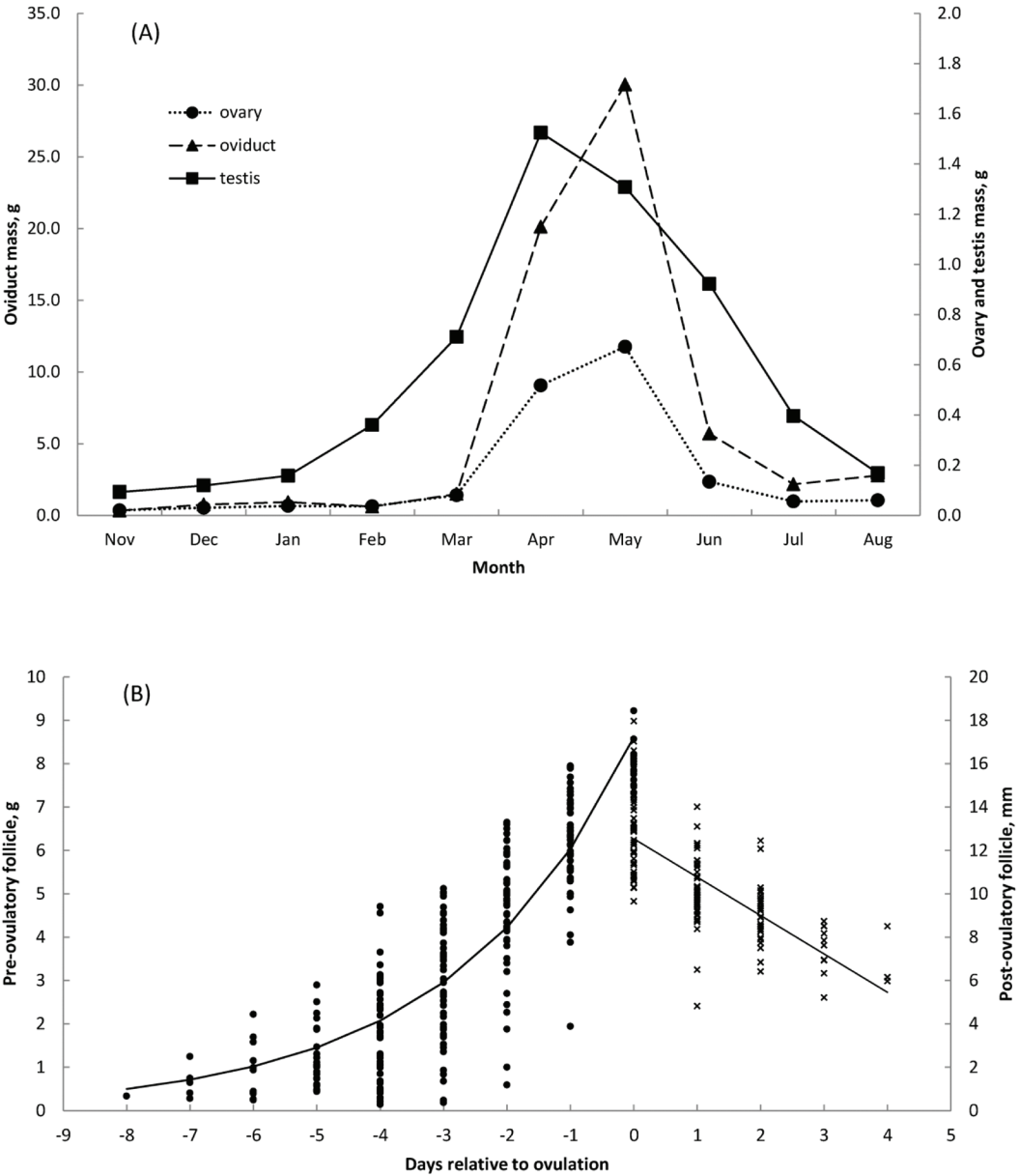


Figure 1. (A) Changes in reproductive organ mass of Double-crested Cormorants (*Phalacrocorax auritus*) over time ($n = 966$ males, $n = 747$ females). (B) Pre- and post-ovulatory follicle progression (solid circles, non-linear trend line $y = 8.6051e^{0.3557x}$, pseudo- $R^2 = 0.76$) and regression (x symbol, linear trend line $y = 12.54 - 1.77x$, $R^2 = 0.55$) relative to day of ovulation ($n = 43$ females).

range in eastern North America occurs during that time. Although we could distinguish breeding females from non-breeding females by the size and shape of their oviduct and ovary development, we could not reliably distinguish breeding males from non-breeding males.

Reabsorption of post-ovulatory follicles was relatively rapid in these cormorants (Fig. 1B), contrasting with observations in waterfowl, where post-ovulatory follicles persist for 30-90 days (Semel and Sherman 1991; Lindstrom *et al.* 2006). Dolbeer and Bernhardt (2003) observed post-ovulatory follicles in

Table 1. Percentage of breeding female Double-crested Cormorants (*Phalacrocorax auritus*) collected from nesting colonies and feeding flocks.

	Nesting Colonies		Feeding Flocks		Z	P-value
	n	% Breeders	n	% Breeders		
Lake Champlain, Vermont ¹	58	93.1	87	63.2	3.94	< 0.001
Leech Lake, Minnesota ¹	39	97.4	31	77.4	2.24	0.025
Eastern USA ²	202	85.1	358	77.9	2.07	0.019

¹Cormorants were collected from nesting colonies and feeding flocks concurrently at each location.

²All cormorants combined, collected during the breeding season from nesting colonies in Alabama, Michigan, Minnesota, New York, and Vermont; and from feeding flocks in Michigan, Minnesota, and Vermont.

Laughing Gulls (*Leucophaeus atricilla*) > 60 days post-ovulation. However, length of time post-ovulatory follicles remain visible following ovulation differs considerably among avian taxa (Semel and Sherman 1991).

We determined the number of eggs a cormorant laid by macroscopic examination of the ovary within 1-2 weeks of initiation of egg laying. Detection of post-ovulatory follicles > 7-14 days post-ovulation would not provide reliable estimates of eggs produced and laid because of the rapid reabsorption of post-ovulatory follicles. The maximum of eight pre-ovulatory follicles observed in some cormorants does not necessarily equate to eight eggs subsequently being laid. Rather, this capacity for additional egg laying exists in the event of nest destruction, egg-oiling, egg predation, or other forms of clutch loss (Korfanty *et al.* 1999).

Differences in the proportion of non-breeding females collected from foraging flocks (22.1%) or directly off nesting colonies (14.9%) exist, and overall we found that 19.5% of females collected from the eastern USA were non-breeding. Due to bias in collections of breeding cormorants directly from colonies, foraging flock collections likely provide the best estimate of the proportion of breeders vs. non-breeders in local populations in this study. Presumably, males would have similar proportions of breeders/non-breeders, but this could not be verified due to rapid proliferation and regression of the testis.

Our findings indicate that the culling of cormorants directly from breeding colonies will remove greater numbers of breeding cormorants than culling from foraging flocks away from colonies. However, the im-

pacts of culling with respect to population modeling efforts are further complicated by evidence that on colonies sex of culled cormorants is biased toward males (Bédard *et al.* 1999; Dorr *et al.* 2014b). These factors combined could lead to more rapid reduction in cormorant numbers than would be expected given proportional culling of breeders and non-breeders and sexes. This rapid decline has been observed at some colony locations where culling has been implemented (Bédard *et al.* 1999; Strickland *et al.* 2011) but not at all locations (Farquhar *et al.* 2012), suggesting other factors including immigration and emigration play a role in outcomes of control efforts. The information in this study on reproductive potential, culling effects and proportion of breeders vs. non-breeders should be considered when evaluating effects of cormorant management on cormorant colonies and the cormorant population in North America.

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