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## Population Ecology

# Population Dynamics of Double-Crested Cormorants in Two Interior Breeding Areas

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**ABSTRACT** Because of rapid population expansion, conflicts between double-crested cormorants (*Phalacrocorax auritus*) and humans have increased, particularly at aquaculture facilities in the Lower Mississippi River Valley (LMRV), United States. Although key demographic information on the Interior population is sparse, management decisions for population reduction are already in place across their breeding range. New evidence suggests the Appalachian Mountains may act as a migration divide for Interior cormorants, causing some birds to migrate between LMRV and the western Great Lakes, whereas others migrate between Florida and the eastern Great Lakes. Most of the banded cormorants recovered near LMRV aquaculture facilities were banded as nestlings at colonies from the central Great Lakes west to the northern Great Plains. We selected 2 geographically distinct Interior cormorant breeding areas: west of the Great Lakes in Lake of the Woods (LOW) and eastern Lake Ontario (ELO), located on either side of the migration divide in the province of Ontario, Canada, to study population dynamics. We used age-specific classes for our mark-recapture analysis (Program MARK) on data collected from 9,498 color-banded cormorants during the breeding seasons of 2000–2008. Adult survival was the same for both areas (LOW =  $0.84 \pm 0.09$  SE, ELO =  $0.83 \pm 0.05$  SE). Finite rates of population growth ( $\lambda$ ) were also similar (LOW = 1.01, ELO = 0.97) and sensitivity analyses indicated that adult survival was the most influential vital rate contributing to  $\lambda$  for both breeding areas. However, young-of-the-year survival estimates were distinctly less in ELO ( $0.19 \pm 0.02$  SE) than in LOW ( $0.45 \pm 0.10$  SE) and sensitivity analysis revealed that young-of-the-year survival played a key role in ELO population growth. Moreover, ELO breeding area fidelity ( $F$ ) was much greater ( $0.94 \pm 0.05$  SE) than the  $F$  estimates for all age classes in LOW (between  $0.68 \pm 0.19$  SE and  $0.80 \pm 0.13$  SE). Considering these regional demographic differences, we recommend that future management efforts be based on migratory flyways within the Interior population. © 2013 The Wildlife Society.

**KEY WORDS** aquaculture, demographics, Great Lakes region, Lefkovich matrix models, mark-recapture models, migration, *Phalacrocorax auritus*, population dynamics, survival estimation.

Double-crested cormorants (*Phalacrocorax auritus*; hereafter, cormorant) are widespread and abundantly distributed within 5 major North American breeding regions: Alaska, Pacific (coastal British Columbia to Mexico), United States and Canadian Interior (Alberta and Utah to St. Lawrence River), North Atlantic (coastal Nova Scotia to Massachusetts), and Florida and Caribbean (Hatch and Weseloh 1999, Wires and Cuthbert 2006). However, not all regions exhibit the same population trends. The Interior population of cormorants is burgeoning (Wires et al. 2001), the North Atlantic population appears to have stabilized (Hatch and

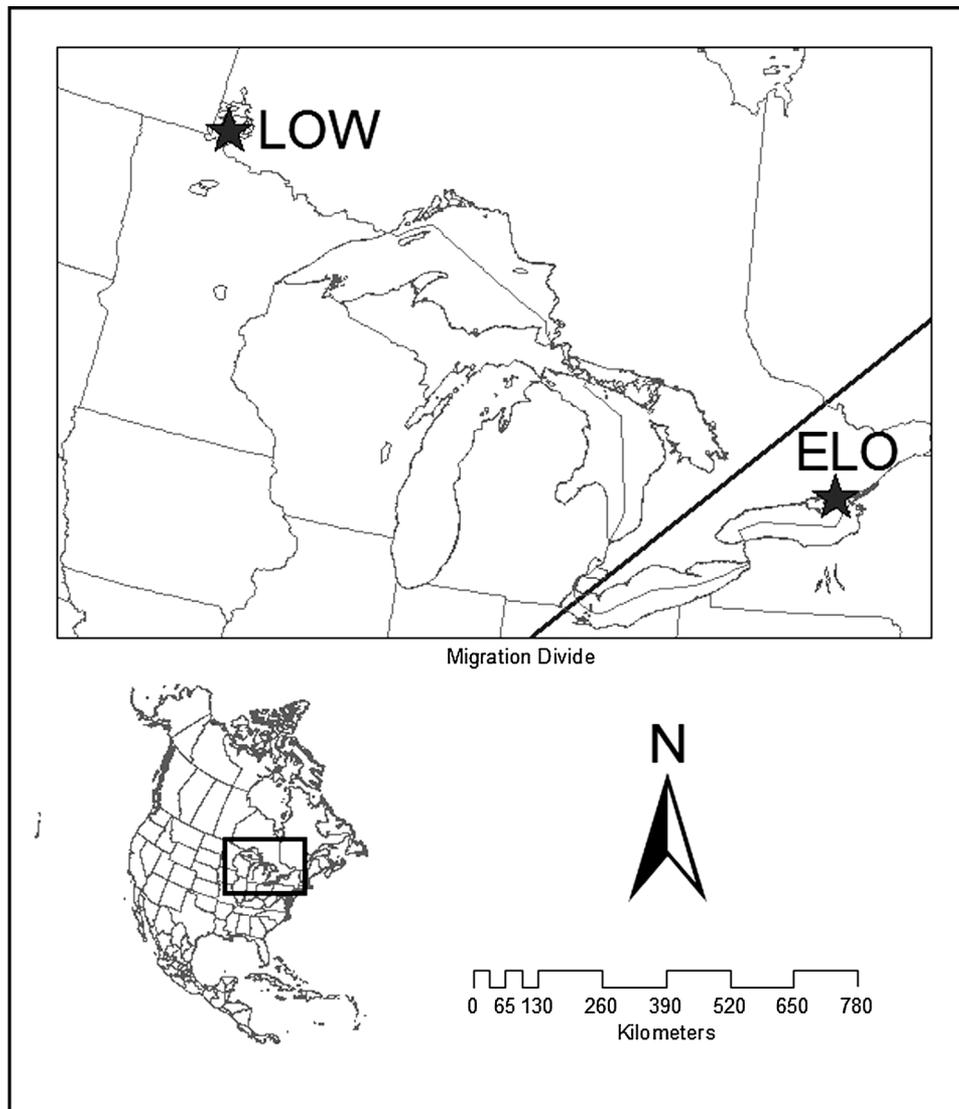
Weseloh 1999), and the Pacific population, although increasing in some areas, is generally declining (Wires and Cuthbert 2006, King et al. 2010). North Atlantic and Interior cormorants are highly migratory, using both the Atlantic and the Mississippi River Flyways, whereas other populations are resident within their breeding range (Dolbeer 1998, Hatch and Weseloh 1999, King et al. 2010). Telemetry studies suggest the Appalachian Mountains may serve as a migratory divide for Interior cormorants across the Great Lakes with western populations migrating to the Lower Mississippi River Valley (LMRV) and eastern populations overwintering in Florida (Fig. 1; Guillaumet et al. 2011).

Interior cormorant populations have increased exponentially over the past 30 years, amplifying conflicts between cormorants and humans (King et al. 2010, Ridgway et al. 2012). Controversy over perceived and documented cormorant impacts to natural and commercial resources is

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**Figure 1.** Location of the 2 double-crested cormorant breeding areas sampled for population characteristics in Ontario, Canada, during 2000 to 2008. Migration Divide, extension of the Application Mountains; LOW, Lake of the Woods; ELO, Eastern Lake Ontario.

particularly acute with the catfish (*Ictalurus punctatus*) aquaculture industry, which began expanding rapidly in the LMRV in 1985 (Bédard et al. 1995, Glahn and Stickley 1995, Glahn et al. 1999, King et al. 2010). Since the 1980s, these piscivorous birds have been increasingly found foraging at commercial aquaculture facilities. In the Mississippi Delta, numbers at the facilities peak in March before migration when 87% of their diet contains catfish (Glahn et al. 1999). Furthermore, a 454% increase in band recoveries from LMRV aquaculture areas has occurred since the mid-1980s and the majority of these recoveries (>90%) originate from breeding grounds west of Lake Huron (King et al. 2010).

Expansion of the aquaculture industry in the LMRV has likely enhanced the food supply for wintering cormorants (Weseloh and Ewins 1994, Glahn et al. 1999, Blackwell et al. 2002, Hebert et al. 2008, King et al. 2010). Studies of cormorants collected in the Mississippi Delta have shown

that they improve their overwinter body condition by foraging at aquaculture facilities (Glahn and Stickley 1995, Glahn et al. 1999). Hebert et al. (2008) also suggested, using sulfur isotope analysis from feathers grown during the winter months, that if cormorants spend at least a portion of the overwintering period foraging at aquaculture facilities, they return to the breeding grounds in better physical condition than cormorants that solely used marine environments.

We explored the population-level implications of a migration divide within the Interior cormorant range. If overwinter foraging on aquaculture facilities enhances cormorant survival and the migration divide separates the Interior population into 2 distinct groups, then we would expect survival of the western populations that have access to these facilities to be greater than their eastern counterparts. Our objectives were to estimate breeding site fidelity, fecundity, and age-specific survival for 2 distinct Interior cormorant breeding areas located on either side of the Great

Lakes migration divide, and develop projection models for these discrete populations to assess the potential influence of a migration divide on Interior cormorant population dynamics. Currently, little is known about cormorant population dynamics and few estimates exist for parameters such as age-specific survival, fecundity, immigration, and emigration between regions (Nettleship and Duffy 1995, Hatch and Weseloh 1999, Wires et al. 2001, Blackwell et al. 2002). Previous studies have used band recoveries to evaluate temporal trends in cormorant survival (Seamans et al. 2012); however, there are many situations in which data of various types (e.g., recaptures and recoveries) can be used together to improve parameter estimate precision and estimate parameters not possible using data from a single source (Burnham 1993). This study is the first extensive cormorant live-encounter dead-recovery banding project of its kind in North America and the most comprehensive study to estimate demographic parameters on a multi-regional scale.

## STUDY AREA

We selected 2 geographically distinct Interior cormorant breeding areas located on either side of the migration divide (the Appalachian Mountains; Fig. 1). The study areas included Lake of the Woods (LOW) near Kenora in the southwestern corner of Ontario (latitude 49.663, longitude -94.507) and eastern Lake Ontario (ELO) near Kingston in the southeastern corner of Ontario, Canada (latitude 44.191, longitude -76.543). Both of these areas contained ground-nesting cormorant colonies on a series of small islands, within approximately 15 km of the corresponding cities listed above. The LOW study area was comprised of 4 islands: Manitou, Lemmon, Island north of Lemmon Island, and Guano Rock. The ELO study area was comprised of 3 islands: Snake, Pigeon, and West Brothers Island. We

treated each island as a replicate within the nesting area (LOW mean distance between islands = 0.96 km ± 0.2 SE, range = 0.42 km–1.56 km; ELO mean distance between islands = 11.86 km ± 4.01 SE, range = 3.83 km–17.0 km). The islands consisted of granite slabs or limestone outcroppings ranging in size from 0.2 ha to 3 ha.

## METHODS

### Banding

Beginning in 2000 in ELO and in 2002 in LOW and continuing through 2008, we color-banded 9,498 pre-fledged cormorants (Table 1; Institutional Animal Care and Use Committee approved U.S. Department of Agriculture Wildlife Services National Wildlife Research Center Study Protocol QA-979, U.S. Geological Survey Bird Banding Lab Permit 20873, Canadian Wildlife Service Bird Banding Permit 10431). Chick growth is rapid until the fledging stage (averaging 35–40 days old), upon which the growth rate levels off (Dunn 1975). Each year during June and July, we captured flightless young cormorants close to fledging age (approx. 30 days old), applied bands, and released them immediately. Each cormorant received a unique United States Geological Survey aluminum band and a field-readable, tri-laminate plastic color leg-band bearing a unique, engraved, alpha-numeric code (Pro-touch Engraving, Inc., Saskatoon, Saskatchewan, Canada). We banded between 220 and 1,200 pre-fledged cormorants per breeding area per year (Table 1). We distributed the banding effort among the various islands according to colony size, with larger colonies receiving more effort. To estimate local mortality at the end of each breeding season, we searched nesting colonies according to their banding effort both visually and with a metal detector to recover any bands of young cormorants that may have died on site.

**Table 1.** Annual summary of double-crested cormorant bands deployed at each breeding area in Ontario, Canada (LOW, Lake of the Woods; ELO, Eastern Lake Ontario), number of hours spent re-sighting, during which part of the breeding season, number of bands recovered (dead) and number of bands re-sighted (alive) for each cohort throughout the study (2000–2008).

| Area  | Year  | No. of bands deployed | Months during which re-sighting occurred | Re-sight effort (hr) | Recovered (dead) | Re-sighted (alive) |
|-------|-------|-----------------------|--|----------------------|------------------|--------------------|
| LOW   | 2002  | 697                   |  |                      | 101              |                    |
|       | 2003  | 751                   |  |                      | 44               |                    |
|       | 2004  | 647                   |  |                      | 26               |                    |
|       | 2005  | 608                   | Jul                                      | 21                   | 49               | 59                 |
|       | 2006  | 659                   | May–Jul, Sep                             | 52.5                 | 36               | 94                 |
|       | 2007  | 400                   | May–Jul, Sep                             | 72                   | 19               | 144                |
|       | 2008  | 279                   | Jul                                      | 21                   | 1                | 50                 |
|       | Total | 4,041                 |  | 166.5                | 276              | 347                |
| ELO   | 2000  | 220                   |  |                      | 15               |                    |
|       | 2001  | 389                   | Aug–Oct                                  | 33                   | 16               | 14                 |
|       | 2002  | 554                   | Apr–Jun                                  | 18                   | 33               | 16                 |
|       | 2003  | 695                   | Apr–Jun                                  | 10                   | 46               | 18                 |
|       | 2004  | 643                   | Apr–Oct                                  | 50                   | 30               | 68                 |
|       | 2005  | 903                   | Apr–Oct                                  | 46                   | 100              | 98                 |
|       | 2006  | 1,200                 | Apr–Oct                                  | 180                  | 244              | 195                |
|       | 2007  | 503                   | Apr–Oct                                  | 146                  | 40               | 344                |
|       | 2008  | 350                   | Apr–Oct                                  | 98                   | 12               | 294                |
|       | Total | 5,457                 |  | 581                  | 536              | 1,047              |
| Total | 9,498 |                       | 747.5                                    | 812                  | 1,394            |                    |

## Re-Sighting

We searched for color-bands by scanning the legs of cormorants with binoculars and a spotting scope. We collected observations from both an elevated blind, erected prior to cormorant nest construction, and by walking through the colony at a distance that did not cause disturbance to nesting birds (the latter, usually during incubation at  $\geq 150$  m). Blinds were located on Island North of Lemmon Island in LOW and Snake Island in ELO. Because each color-band had a unique alpha-numeric-code, we could determine the age and natal colony of each re-sighted bird.

Re-sighting effort varied between sites and among years (Table 1). At LOW in 2005, we re-sighted bands only during the 2 days prior to banding in July. During 2006 and 2007, we made observations from the blind once a month over the course of the breeding season: in May during nest construction and initial laying, in June during late-incubation, in July just before chick fledging, and in September after fledging at the end of the season. In 2006, we spent a continuous interval of 24 hours in the blind each visit, conducting observations during periods of daylight. In 2007, we extended the observations over 2 days to span 24 hours of consecutive daylight. In 2008, we only conducted observations prior to banding in July for a consecutive 24-hour daylight period.

In ELO, we collected opportunistic re-sight observations from 2001 to 2003 while walking through the colonies. We erected an observation blind on Snake Island in 2004 and collected irregular observations from the blind during 2004 and 2005. From 2006 to 2008, we systematically visited Snake Island at least once per month beginning in April, comparable to re-sighting effort at LOW but more frequently when possible, throughout the breeding season into October (Table 1).

## Survival Estimates

We used a Burnham joint live-encounter dead-recovery model (Burnham 1993) in Program MARK (White and Burnham 1999) to estimate survival ( $S$ ), the probability of a live bird being re-sighted and the band read ( $p$ ), the probability that a bird died and its band was recovered ( $r$ ), and breeding area fidelity ( $F$ ) for banded cohorts in LOW and ELO. Because of the variability in re-sighting effort among years or sites, we only considered time-specific ( $t$ ) models for  $p$ ; we considered both time-specific ( $t$ ) and constant ( $-$ ) models for  $S$ ,  $F$ , and  $r$ . We did not observe cormorants in 2003 and 2004 in LOW; therefore, we fixed those 2  $p$  parameters to 0 for all of the models in the model set. We grouped cormorants into age-specific classes based on surviving to the next breeding season (e.g., the first age class was young-of-the-year [age 0 yr] surviving to the next breeding season the following year). We considered models with 2 ( $a_2$ ; ages 0 and  $\geq 1$  yr), 3 ( $a_3$ ; ages 0, 1, and  $\geq 2$  yr), and 4 ( $a_4$ ; ages 0, 1, 2, and  $\geq 3$  yr) age classes. Although banding occurred later in the season, we used the beginning of the breeding season (1 Apr) as the anniversary date.

For each location, we chose a model set with all possible parameter combinations to avoid any loss of information ( $n = 20$  models). We ran a median  $c$ -hat goodness-of-fit test on the global model and then adjusted all the models in the set for overdispersion ( $c$ -hat LOW = 3.58,  $c$ -hat ELO = 4.38). We used the quasi-likelihood form of Akaike's Information Criterion corrected for sample size (QAIC<sub>c</sub>) based on information-theoretic methods to select the models for parameter estimation (Burnham and Anderson 2002). We considered models with the lowest QAIC<sub>c</sub> values ( $\Delta\text{QAIC}_c \leq 2$ ) to be the most parsimonious models to approximate the data, given the set of models considered. We averaged parameter estimates across candidate models using QAIC<sub>c</sub> weights. With each model-averaged survival estimate, Program MARK also calculated a 95% confidence interval, which we used to assess significant differences in parameter estimates between breeding areas.

## Reproduction

At the more northerly nesting area (LOW), cormorants generally initiate nesting about 2–3 weeks later than cormorants in the lower Great Lakes (ELO; Ewins et al. 1995). During colony observations, we classified banded birds as breeding if they were seen defending a territory against conspecifics, bringing nesting material to a mate, nest building, incubating eggs, or brooding or attending nestlings. Cormorants are monomorphic; therefore, we were not able to determine the sex of banded birds, or the colony sex ratio.

With the exception of ELO colonies in 2008, each year at the time of banding (during the fledging stage of chick development), we conducted a census of all nests and estimated the number of fledglings in the colony using direct observation. We used a technique modified from Weseloh et al. (1995) to estimate colony-specific fledge rates (CFR = number of fledglings/nest/colony) with the following equation:

$$\text{CFR} = \frac{F1}{Tn - An}$$

We divided the total number of fledglings in the colony (F1) by the total number of nests ( $Tn$ ) minus the number of active nests ( $An$ ; 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).

We used fledging rates as a proxy for fecundity estimates. We calculated area-specific fecundity as the number of female offspring produced per nest. A breeding female is associated with each nest in a colony; however, some females may fledge 0 young. To consider all nesting attempts, we included all nests within the colony that did not contain eggs or naked young ( $Tn - An$ ) for our colony-specific fledge rate estimate; we assumed that some of these nests potentially fledged 0 chicks. By dividing the number of fledglings by the number of nests, including nests that may have fledged 0 chicks, we could calculate the number of fledglings produced per nest. Colony-specific fledge rates from each area were

averaged together to create area-specific fledge rates (total number of offspring per nest per breeding area). We assumed a 1:1 sex ratio and divided the total offspring by 2 (Yackel Adams et al. 2007) to estimate the number of female offspring produced per nest and used this as a constant area-specific fecundity rate.

### Population Models

For each breeding area, we built and analyzed matrix models for the female half of the population and performed sensitivity and elasticity analyses in Microsoft Excel© 2007 using the PopTools add-in (version 2.7, www.poptools.org, accessed 5 Jun 2007). The models were  $4 \times 4$  grids of stage-classified matrices (Leslie 1945, Lefkovich 1965) based on our estimates of survival and fecundity. Based on the work of Seamans et al. (2012), density-dependent factors had no significant effect on survival. For model simplification, we assumed breeding began at the age of 3 years (van der Veen 1973). We used a joint live-encounter dead-recovery model to minimize the bias associated with permanent emigration from the study area. By using  $S$ , we included individuals in the population even if they permanently emigrated; therefore, emigration should have little to no influence on the matrix models. We could not accurately measure immigration because few sources of color-banded birds occurred outside the study areas. Therefore, we assumed immigration was minimal and thus had no real impact on the matrix models.

We grouped cormorants into 4 age classes. The first age class was young-of-the-year (age 0) surviving to the next breeding season. The second and third age classes, respectively, were birds aged 1 and 2 years that survived to the next breeding season. The fourth age class was comprised of birds aged  $\geq 3$  years. Similar to Blackwell et al. (2002), our decision to pool the fourth age class was influenced by Program MARK's preferential QAIC<sub>c</sub> ranking of models with 3 and 4 age classes.

## RESULTS

In LOW, we recorded 69 1-year-olds, 73 2-year-olds, 78 3-year-olds, and 68 birds aged 4 years and older. In ELO, we recorded 92 1-year-olds, 205 2-year-olds, 153 3-year-olds, and 215 birds aged 4 years and older. Of the 953 color-

banded cormorants observed during the 2006 to 2008 breeding seasons, we recorded 252 (26.4%) as breeding (18% in LOW and 30% in ELO). The mean age of birds classified as breeding at LOW was  $3.20 \pm 0.12$  SE and  $3.81 \pm 0.14$  SE at ELO.

### Lake of the Woods

We deployed 4,041 bands and observed 347 (8.6%) live color-banded cormorants in LOW from 2002 to 2008 (Table 1). Area-specific fledge rates were 1.35, 1.61, and 1.05 chicks per nest in 2006, 2007, and 2008, respectively; the average fledge rate was 1.34 chicks per nest producing a fecundity estimate of 0.67 female chicks fledged per nest. Based on  $\Delta\text{QAIC}_c$  values, the 3 models with the best fit specified 3 ( $a_3$ ; ages 0, 1, and  $\geq 2$  yr) and 4 ( $a_4$ ; ages 0, 1, 2, and  $\geq 3$  yr) age classes, 1  $a_3$  model with constant  $F$  and the other with time-specific  $F$ , and all with time-specific  $p$  and  $t$  (Table 2). Survival estimates were 0.45 ( $\pm 0.10$  SE) for the first age class (young-of-the-year, age 0), 0.63 ( $\pm 0.09$  SE) for the second age class (age 1), 0.87 ( $\pm 0.07$  SE) for the third age class (age 2), and 0.84 ( $\pm 0.09$  SE) for the fourth age class (age  $\geq 3$  yr; Fig. 2). We estimated cormorant age-specific breeding site fidelity to be 0.68 ( $\pm 0.19$  SE) for the first age class, 0.80 ( $\pm 0.13$  SE) for the second and third age classes, and 0.70 ( $\pm 0.16$  SE) for the fourth age class. Re-sight probabilities ( $p$ ) ranged from 0.01 ( $\pm 0.01$  SE) to 0.32 ( $\pm 0.09$  SE) and recovery probabilities ( $r$ ) ranged from 0.01 ( $\pm 0.01$  SE) to 0.25 ( $\pm 0.06$  SE).

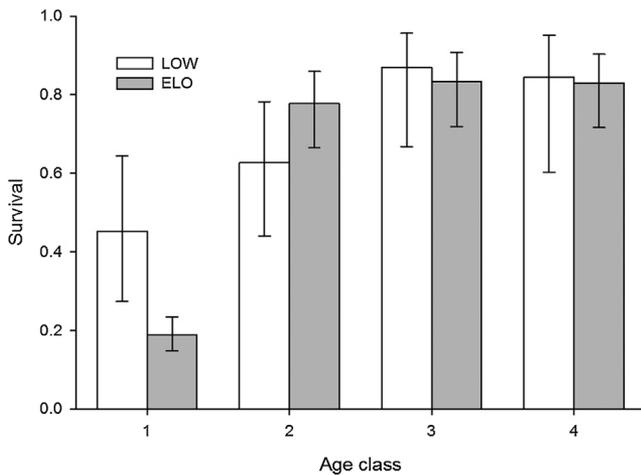
Sensitivity and elasticity analysis (Caswell 2001) of the Lefkovich matrix (Table 3) revealed that adult survival (the fourth age class, age  $\geq 3$  yr) was the most responsive vital rate to change population growth rate (sensitivity = 0.68, elasticity = 0.57). A 50% reduction in adult survival would reduce the population's growth by 23%. A 100% reduction in fecundity resulted in a 16% reduction in population growth. However, a combination of these 2 decreased parameters would reduce cormorant population growth by 58%. We estimated the finite rate of population change ( $\lambda$ ) to be 1.01 with a generation time of 9.33 years.

### Eastern Lake Ontario

We deployed 5,457 bands and observed 1,047 (19.2%) live color-banded cormorants in ELO from 2000 to 2008

**Table 2.** The top 5 models from each of the set of 20 models used for demographic estimates of double-crested cormorants in Lake of the Woods (LOW) and eastern Lake Ontario (ELO), Ontario, Canada. We modeled parameters in Program MARK with the Burnham joint live-encounter dead-recovery model, ranked models based on the quasi-likelihood form of Akaike's Information Criterion corrected for sample size (QAIC<sub>c</sub>), and adjusted for overdispersion with c-hat estimation (LOW = 3.58; ELO = 3.58). We banded cormorants as young-of-the-year from 2000 to 2008. Model parameters included survival ( $S$ ) for 2 ( $a_2$ ; age 0 and  $\geq 1$  yr), 3 ( $a_3$ ; age 0, 1, and  $\geq 2$  yr), and 4 ( $a_4$ ; age 0, 1, 2, and  $\geq 3$  yr) age classes with different combinations of time-specific ( $t$ ) or constant ( $-$ ) re-sight probability ( $p$ ), recovery probability ( $r$ ), and site fidelity ( $F$ ).

| Area | Model                    | QAIC <sub>c</sub> | $\Delta\text{QAIC}_c$ | QAIC <sub>c</sub> weights | No. of Parameters | QDeviance |
|------|--------------------------|-------------------|-----------------------|---------------------------|-------------------|-----------|
| LOW  | { $S(a_3)p(t)r(t)F(-)$ } | 1360.393          | 0.000                 | 0.447                     | 15                | 86.979    |
|      | { $S(a_4)p(t)r(t)F(-)$ } | 1361.641          | 1.248                 | 0.239                     | 16                | 86.211    |
|      | { $S(a_3)p(t)r(t)F(t)$ } | 1362.252          | 1.859                 | 0.176                     | 19                | 80.768    |
|      | { $S(a_4)p(t)r(t)F(t)$ } | 1363.723          | 3.330                 | 0.085                     | 20                | 80.219    |
|      | { $S(a_2)p(t)r(t)F(-)$ } | 1365.192          | 4.799                 | 0.041                     | 14                | 93.793    |
| ELO  | { $S(a_3)p(t)r(t)F(-)$ } | 2279.885          | 0.000                 | 0.425                     | 21                | 217.519   |
|      | { $S(a_2)p(t)r(t)F(-)$ } | 2280.025          | 0.140                 | 0.396                     | 20                | 219.673   |
|      | { $S(a_4)p(t)r(t)F(-)$ } | 2281.787          | 1.901                 | 0.164                     | 22                | 217.407   |
|      | { $S(a_3)p(t)r(t)F(t)$ } | 2287.990          | 8.105                 | 0.007                     | 27                | 213.532   |
|      | { $S(a_2)p(t)r(t)F(t)$ } | 2288.712          | 8.827                 | 0.005                     | 26                | 216.271   |



**Figure 2.** Survival estimates with upper and lower 95% confidence intervals for 2 breeding areas within the Interior double-crested cormorant breeding range in Ontario, Canada. Survival represented as a rate. We banded cormorants as young-of-the-year and grouped them into 4 age classes: age class 1 (<1 year), 2 (1–2 years), 3 (2–3 years), and 4 ( $\geq 3$  years). LOW, Lake of the Woods; 4,041 bands deployed, 347 live color-banded cormorants observed from 2002 to 2008; ELO, Eastern Lake Ontario; 5,457 bands deployed, 1,047 live color-banded cormorants observed from 2000 to 2008.

(Table 1). Area-specific fledge rates were 2.16 in 2006 and 1.93 in 2007 (not estimated in 2008); the average fledge rate was 2.04 chicks per nest producing a fecundity estimate of 1.02 female chicks fledged per nest. Based on  $\Delta QAIC_c$  values, the 3 models with the best fit to the data had 2 ( $a_2$ ; ages 0 and  $\geq 1$ ), 3 ( $a_3$ ; ages 0, 1, and  $\geq 2$ ), and 4 ( $a_4$ ; ages 0, 1, 2, and  $\geq 3$  yr) age classes, all with time-specific  $p$  and  $t$  and constant  $F$  (Table 2). Survival estimates were 0.19 ( $\pm 0.02$  SE), 0.78 ( $\pm 0.05$  SE), 0.83 ( $\pm 0.05$  SE), and 0.83 ( $\pm 0.05$  SE) for the first (young-of-the-year, age 0), second (age 1), third (age 2), and fourth (age  $\geq 3$  yr) age classes, respectively (Fig. 2). The best models preferred constant breeding area fidelity, which we estimated to be 0.94 ( $\pm 0.05$  SE) for all age classes. Re-sight probabilities ( $p$ ) ranged from 0.05 ( $\pm 0.06$  SE) to 0.45 ( $\pm 0.07$  SE) and recovery probabilities ( $r$ ) ranged from 0.04 ( $\pm 0.02$  SE) to 0.26 ( $\pm 0.03$  SE).

Sensitivity and elasticity analysis of the Lefkovich matrix (Table 3) revealed that although young-of-the-year survival (age 0) played a key role (sensitivity = 0.514; however, elasticity = 0.100), adult survival (age  $\geq 3$ ) was the most responsive vital rate to change population growth rate (sensitivity = 0.701, elasticity = 0.602). A 50% reduction in adult survival would reduce the population's growth by 24%. A 100% reduction in fecundity resulted in a 14% reduction in population growth. A combination of these 2 decreased parameters would reduce cormorant population growth by 55%. We estimated the finite rate of population change ( $\lambda$ ) to be 0.97 per year with a generation time of 9.40 years.

## DISCUSSION

Adult survival estimates did not differ between LOW and ELO; however, population growth models indicated a stable population in LOW and a slightly declining population in ELO. Adult survival estimates from this study (83–84%)

**Table 3.** Stage-classified projection matrix for 2 breeding areas of Interior double-crested cormorants in Ontario, Canada. We considered cormorants to be reproductively mature at 3 years of age. We estimated fecundity using fledge rates from the 2006 to 2008 breeding seasons, divided by 2 to account for an assumed 1:1 sex ratio. We generated survival estimates in Program MARK from birds banded as young-of-the-year (age class 1). We grouped cormorants into 4 age classes: age class 1 (<1 year), 2 (1–2 years), 3 (2–3 years), and 4 ( $\geq 3$  years). The first row represents fecundity (sensitivity) [elasticity]; the diagonal represents age-class survival (sensitivity) [elasticity].

| Area | 1                           | 2                           | 3                           | 4                           |
|------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| LOW  | 0                           | 0                           | 0                           | 0.668<br>(0.163)<br>[0.108] |
|      | 0.452<br>(0.241)<br>[0.108] | 0                           | 0                           | 0                           |
|      | 0                           | 0.627<br>(0.174)<br>[0.108] | 0                           | 0                           |
|      | 0                           | 0                           | 0.869<br>(0.125)<br>[0.108] | 0.845<br>(0.675)<br>[0.567] |
| ELO  | 0                           | 0                           | 0                           | 1.021<br>(0.094)<br>[0.100] |
|      | 0.187<br>(0.514)<br>[0.100] | 0                           | 0                           | 0                           |
|      | 0                           | 0.777<br>(0.124)<br>[0.100] | 0                           | 0                           |
|      | 0                           | 0                           | 0.833<br>(0.115)<br>[0.100] | 0.829<br>(0.701)<br>[0.602] |

were similar to those reported in other parts of the breeding range of Interior double-crested cormorants. Ludwig (1984) estimated 85% adult survival in Michigan and the upper Great Lakes, Blackwell et al. (2002) estimated 88% adult survival for all of Lake Ontario, and Duerr (2007) estimated 82% adult apparent survival in Lake Champlain. Although sensitivity analyses emphasized adult survival as the most influential vital rate contributing to  $\lambda$ , our projection matrix conclusions suggest, as other studies have suggested, that a joint reduction in adult survival and fecundity will have the greatest efficacy for reducing cormorant population growth (Bédard et al. 1995, Strickland et al. 2011, Ridgway et al. 2012).

Interestingly, fecundity and young-of-the-year survival differed between the 2 breeding areas, suggesting differences in their population dynamics. In each region, recruitment is confounded with a different limiting factor. For LOW, it was fledging, whereas for ELO, it was first-year survival. Although ELO produced almost 50% more female offspring each year, only 20% of those offspring survived their first year. LOW produced only a fraction of the amount of female offspring, but 45% of those offspring survived their first year. The potential interacting influences of survival and fecundity on recruitment may explain the slight divergence in  $\lambda$  between the 2 populations. Fecundity can be influenced by many different factors such as female investment (Marshall

and Uller 2007), nest failure by predators (Oro et al. 2006), and weather (Velando and Freire 2002, LaHaye et al. 2004), all of which may explain our regional differences, but are beyond the scope of this study. Superior foraging opportunities at nest site locations have been shown to increase fecundity for cormorants at Lake Champlain (Duerr 2007), perhaps this explains why fecundity is greater in ELO.

Differential survival between these groups supports the idea that the Appalachian Mountains might act as a migration divide. The ELO cormorants may exclusively overwinter in Florida (Guillaumet et al. 2011), whereas LOW cormorants benefit from enhanced overwinter foraging at LMRV aquaculture facilities, which may dampen the selection pressures faced during their first year of life (Glahn et al. 1999). However, the United States Fish and Wildlife Service began issuing individual depredation permits in 1987, and a standing Depredation Order (50 CFR 21.47) in 1998, permitting the lethal removal of cormorants at aquaculture facilities; therefore, cormorants of all ages likely face a greater probability of being shot while foraging at LMRV aquaculture facilities. We suggest a more definitive measure, such as specific wintering ground stable isotope markers, be explored. In doing so, management efforts can focus on population segments specifically responsible for the economic and natural resource damage.

Concurrent management practices to suppress the population on the breeding grounds also have the potential to influence cormorant movements and population dynamics. Dispersal may be restricted because of a lack of available habitat other than the natal site. The constant breeding area fidelity ( $F$ ) estimate for ELO was much greater than the  $F$  estimates for all ages in LOW. Strong site fidelity at ELO study sites, where no management activities were employed, may be the result of active management occurring at other sites in the region (Duerr et al. 2007). In response to escalating concerns about prolific cormorant populations in New England and Ontario, several state, federal, and provincial agencies began actively managing cormorants in 1994. Varying degrees and combinations of hazing, nest removal, egg oiling, and adult culling were used in Lake Ontario, Lake Champlain, Oneida Lake, and the Saint Lawrence River throughout the course of our study (Duerr et al. 2007, McCullough et al. 2008, Ontario Parks 2008, Lemon 2010, Strickland et al. 2011). Cormorants display a high affinity to undisturbed locations with high reproductive output, such as our ELO study sites (Duerr et al. 2007, Strickland et al. 2011). In contrast, no cormorant management activities were in place in LOW or the surrounding areas before or during our study (Ontario Ministry of Natural Resources 2006). Weak site fidelity at LOW may result from low fecundity rates and no restrictions on dispersal. Unfortunately, we are unable to make direct comparisons between our fidelity estimates and other studies because many studies only report model significance and not actual values for vital rates. However, our ELO estimate appears to be similar to Aebischer's (1995) report that 95% of European shags (*Phalacrocorax aristotelis*) nest within a 12-km radius of the natal colony in eastern Britain and Velando and Freire's

(2002) report that shags breeding at the Cies Islands off the coast of Spain "showed a high site fidelity."

Immigration may explain why ELO colonies persist despite low recruitment rates. During the breeding seasons of 2004 to 2008, we collected 81 data points from the re-observation of 65 uniquely banded cormorants marked in colonies from New York and Vermont ( $n=52$ ; including Oneida Lake, Lake Champlain, and Little Galloo Island), Lake Huron ( $n=10$ ; including Georgian Bay and North Channel), and Green Bay, Lake Michigan ( $n=3$ ). Although we did not include these birds in our survival models, they represent 7.5% of the banded birds we observed in ELO during the breeding seasons of 2004 to 2008. The birds observed from Lake Huron may have emigrated because of large-scale management activities, namely egg oiling, during 2002–2005 (Ridgway et al. 2012). In 2006, Wisconsin Department of Natural Resources also began oiling eggs in Lake Michigan (U.S. Department of Agriculture 2009). Further investigation is needed to determine the extent to which colonies in ELO interact with colonies across the Great Lakes region. We did not observe any banded cormorants from other locations in LOW during the course of our study. Except for a few small banding projects in Lake Michigan, we are unaware of any other banding projects occurring in the area during this time.

The parameters used in our matrix models were conservative. For example, our models specified that breeding initially occurred at 3 years of age. The data showed that a proportion of the birds did breed in their second year (6% in LOW and 24% in ELO); however, we are uncertain how successful these breeding attempts were. Furthermore, our models were simplified by assuming immigration and emigration were minimal. This may be the case in LOW, but we observed immigration in ELO. To account for the potential bias associated with permanent emigration from the study area, we used a joint live-encounter dead-recovery model. By using  $S$ , we included individuals in the population even if they permanently emigrated. Nevertheless, when dealing with a dispersive species like cormorants, survival estimates suffer from an unknown bias due to permanent emigration away from the study area (Frederiksen and Bregnballe 2000). We used fledging rates as a proxy for fecundity estimates, thus our assumptions were associated with an inherent level of bias. Re-nesting, for example, is common following the loss of a complete clutch (Hatch and Weseloh 1999); however, late season nests experience reduced fledging rates (McNeil and Léger 1987). Although this is not a true estimate of fecundity, it is the closest estimate we could perform with our limited time in the colonies. Researcher presence during this study may have influenced cormorant fledge rates because of increased disturbance and resultant gull depredation (Kury and Gochfeld 1975, Ellison and Cleary 1978), although we believe the impact to be minimal based on observations. Uneven re-sighting effort across years may have introduced selection bias into our study as well; however, by including multiple years of opportunistic band re-sight data in our models, we had considerable improvement in the precision of parameter estimates. To complete a more comprehensive

age-specific matrix model for the Interior double-crested cormorant, color-banding efforts should continue for another 10–15 years to encompass the bird's entire lifespan. Regardless of the limitations, these models provide a biologically sound representation of cormorant population dynamics and a tool by which managers may evaluate the potential effects of different policy decisions.

## MANAGEMENT IMPLICATIONS

Based on the results of this study, differences in fecundity and young-of-the-year survival estimates between the 2 regions suggest that asymmetry exists in Interior cormorant population dynamics. When dealing with any migratory species over a large spatial scale, this example highlights the importance of thoroughly understanding a population's dynamics before applying broad sweeping management decisions. Case in point, if reducing cormorant numbers is the desired result, managers may choose to limit reproductive success in ELO where fecundity is high and strong site fidelity coupled with surrounding management activities has the potential for creating an ecological trap (see Duerr et al. 2007). On the other hand, concentrating management efforts on the adult segment of the population in LOW, which has low fecundity and weak site fidelity, may prove more effective at reducing population numbers. With discrepancies in population dynamics across the breeding range, we recommend that future Interior cormorant population management efforts be structured along migratory flyways (Hebert et al. 2008, Guillaumet et al. 2011).

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